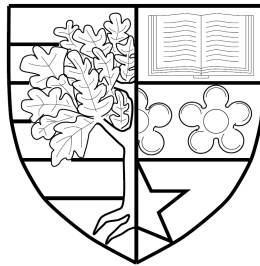


Mathematical Models for Red Squirrel Conservation

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Abstract

In this thesis we develop mathematical models to understand the process of ecological invasion when the invading species also carries a disease that is harmful to the native species. In particular we focus on a key case study system of the invasion of grey squirrels and replacement of red squirrels in the UK, in which the shared disease, squirrelpox, has been suggested as a key driver of the rapid expansion of grey squirrels.

Our initial study focused on examining the viability of red squirrels in the stronghold forests of Kidland and Uswayford in Northumberland. These are commercially managed forests that Forestry Commission England manage to improve red squirrel population viability. Through close collaboration with the Forestry Commission, we developed a mathematical model that could test squirrel population viability for a range of felling and replanting strategies. Our findings have been used to direct the forest design plans that will be implemented in these forests.

Our second study used spatial, stochastic modelling techniques to model the replacement of red squirrels and subsequent control of grey squirrels on the Isle of Anglesey. Our findings indicated that the replacement of red squirrels by grey squirrels on the island was largely driven by competitive interactions. However, on a local level squirrelpox epidemics could occur and lead to mortality in red squirrel populations. Our model was also fitted to data on the control and eradication of grey squirrels and reintroduction of red squirrels that took place on the Isle of Anglesey between 1998-2013. Our fitted model was then used to examine the best conservation strategies to protect the red squirrels on Anglesey.

Our final study compared key findings on the process of disease-mediated invasion in deterministic and stochastic model frameworks. The deterministic frameworks predict that a wave of disease can spread through a native population in advance of a wave of replacement of the invading species. A stochastic representation of this system indicated that this wave of disease in advance of the wave of replacement may not occur if the disease is too virulent to the native species. However, if the disease is supported by the invading species, it will still mediate the invasion at the interface between the native and invading species where local epidemic disease outbreaks can occur.

In general this thesis shows that mathematical models are powerful tools for the conservation management of native species under threat from invasion.

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Chapter 1

Introduction

Introductions of non-indigenous species can have detrimental effects on the natural ecosystem, often resulting in economic and environmental problems (Strauss et al., 2012; Kolar and Lodge, 2001; Manchester and Bullock, 2000). An “indigenous” (or “native”) species is taken to be one that occurs naturally in the area, dispersing independently without human interference. Generally, it is considered to have been established prior to Neolithic times - in the UK, prior to man arriving about 8000 years ago. “Non-indigenous” (or “non-native”) species are therefore species that do not naturally occur in the area, with humans often mediating their translocation, deliberately or inadvertently from their native range to new areas in which colonization has occurred (within the last 8000 years in the UK) (GB Non-native species secretariat, 2017). Such species, which successfully establish in new areas and have serious negative impacts on native species, are known as invasive non-native species (Manchester and Bullock, 2000). Invasive species introductions have been increasing since human migration and trade increased around the world in around 1500 AD (Manchester and Bullock, 2000), with developments in marine transport leading to invasive species acting as “stowaways” crossing previous geographical barriers. There have also been many deliberate species introductions, including ornamental species that were originally for exhibition or as pets, and targeted introductions in the farming and agricultural industry. With increased globalisation, the number of species being transported out-with their native range is rising (Kolar and Lodge, 2001) and therefore increased emphasis must be placed on assessing how introduced species can affect native species.

1.1 Impacts of non-indigenous species

The effects of non-indigenous species vary considerably depending on the specific species and environment being invaded. Multilevel impacts affecting the well being

of society are observed including human, animal and plant health, food and fuel production and regulation of the climate, water, soils and pollution (McLaughlan et al., 2014). Marked effects on the native biodiversity have been observed in detail in some situations. Non-indigenous species can have competitive impacts on indigenous species for resources such as water, nutrients or territories (Strauss et al., 2012; Manchester and Bullock, 2000). Non-indigenous species may also damage native vegetation and drainage due to feeding or nesting habits, while altering food webs potentially by predation. Hybridisation with native species may occur and non-native diseases can also be introduced with the non-native species, which may have detrimental effects on native species. For example the introduction of the predacious Nile perch (*Lates niloticus*) in the 1950s in Lake Victoria, East Africa led to catastrophic vertebrate extinction, with over 200 species of fish becoming extinct since (Kolar and Lodge, 2001). Herbivores can have detrimental effects on native plant populations due to grazing and trampling (Manchester and Bullock, 2000), highlighted by the example of the Canada goose (*Branta canadensis*), which damages native reed beds, salt marshes and other vegetation vital to native species (Watola et al., 1996). Additionally, alterations to the water table, soil properties and vegetation structure can make habitat unsuitable for native species. Introduced species can alter food web interactions. For example, predators and scavengers like shags are attracted by high densities of farmed fish in the UK, with wild indigenous fish in waters near farms then affected by increased predation (Carss, 1993). In the US, non-indigenous species are considered the primary threat to 42% of the species listed as threatened or endangered (Pimentel et al., 2000) with a cost to the US economy in excess of \$138 billion per year.

However, it is important to note that most potential invaders die in transit or soon after release (Kolar and Lodge, 2001). While non-indigenous species can cause a variety of these problems, others can be beneficial or have no known detrimental effect on the natural environment they have moved to. Therefore, it is important to evaluate the different ways in which the non-native species impacts the ecosystem services before deciding on management practices (McLaughlan et al., 2014). It is thought that only approximately 10% of non-indigenous species may cause problems, either to the natural environment or economically (Manchester and Bullock, 2000). Management of all native and non-native species should be considered on a case by case basis based on the historical and ecological circumstances of each species in each location, not just focusing on removing species as they are not native (Lundberg, 2010). Better evaluation of the positive and negative effects species have on ecosystems are required to prioritise management (McLaughlan et al., 2014). Preventing potentially detrimental invasions is always the preferred option so there is a need to understand the invasion process and the determinants of invasion success

(Prenter et al., 2004; McLaughlan et al., 2014).

1.2 Invaders and invasibility

To investigate reasons why some invaders succeed, the general characteristics of successful invaders are considered alongside characteristics of the habitat that aid/hinder invaders establishing. A non-native species has a higher probability of establishing viable populations in areas with a similar climate and ecology to its native regions in which they can survive (Di Febbraro et al., 2013). Vertebrate invaders often have generalist feeding habits, short generation times and are flexible with the physical conditions that they can survive in (Manchester and Bullock, 2000), while successful invading birds often have a larger clutch size than similar native species and are unlikely to have long distance migrations (O'Connor et al., 1986). Plant invaders may have advantages over native species such as faster growth, more frequent seedling and greater seed mass (Rejmanek and Richardson, 1996). Communities can be characterised in terms of invasibility - the susceptibility of an environment to the colonization of species not currently resident in that area (Davis et al., 2005). Disturbed habitats (for example urban wasteland and arable fields) are generally more susceptible to plant invasions, so such areas often have a higher proportion of non-indigenous species than, for example, native, unmanaged woodland (Smallwood, 1994). Aggression and dominance of native animals will also play a part alongside the supply of resources (Davis et al., 2000). Climatic changes are also thought to be a large factor in triggering alterations to species habitat ranges, often resulting in invasive species successfully colonizing areas that were previously out of their range (Rosenzweig et al., 2007). Climate driven changes that cause fluctuation in resource availability are linked to the invasibility of certain habitats and ecosystems (Davis et al., 2000). For example, it is predicted that climate change will greatly influence populations of indigenous species in sub-Antarctic areas as warmer climates will allow exotic species to become established (Rosenzweig et al., 2007).

1.3 Disease-mediated invasion

The role of parasites in determining invasion success is becoming increasingly recognised. In some instances parasites may benefit the native species and prevent the invasion of new species. Transmission of parasites from natives to invaders may help prevent invasions being successful as the non-indigenous species may have little resistance. For example, native diseases can prevent farm animals from flourishing in non-native ranges, such as cattle in Africa being limited by trypanosomiasis (Leak, 1998). Also if the invader is not a good reservoir host for the native parasite, the

invader's presence could decrease the infection prevalence in the native population. The increased diversity in species can "dilute" the impact of the disease. The more diverse the community, the higher the proportion of potential incompetent reservoir hosts, which may have the effect of reducing infection prevalence of the disease, so therefore the presence of additional, non-native species may reduce the impact of a disease in a native species. Lyme disease is an example of a vector-borne disease in which the impact of a parasite can be diluted by species diversity (Ostfeld and Keesing, 2000). The disease is transmitted by ticks to humans. The ticks become infected by the bacteria *Borrelia sp* during feeding on a wide range of mammalian, avian and reptilian hosts, with the white footed mouse (*Peromyscus leucopus*) being highly efficient at infecting ticks in North America. Species-poor vertebrate communities are characterized by a high relative abundance of white-footed mice, while species-rich communities have a higher relative abundance of non-mouse species that are poorer disease reservoirs and hence will dilute the impact of infection and in turn, reduce the risk of human exposure to Lyme disease.

Parasites may also benefit the invasive species. When a non-indigenous species moves to a new area, it may leave behind parasites and natural enemies, leading to a higher demographic success of invaders and potentially a competitive advantage over natives. This is called the "enemy release hypothesis" and has been supported by empirical evidence (Prenter et al., 2004). A study by Torchin et al. (2003) compared the number of parasites of 26 native and non-native species including molluscs, crustaceans, fish, birds, mammals, amphibians and reptiles. Invaders were found to have roughly half the number of parasites as native species, with the prevalence of each parasite generally lower in introduced species too (Torchin et al., 2003). However, the lasting benefit of this parasite loss depends on the reasons for the loss. Invaders may lack parasites as a result of low population density due to their recent translocation. Its parasites may arrive in subsequent invasions and establish when the population reaches a critical level, thus removing the competitive advantage originally present.

The enemy release hypothesis does not explain all invasions, in particular plant invasions. Alternatively, the "accumulation of local pathogens" hypothesis was proposed by Eppinga et al. (2006). This is based on the idea that non-indigenous plant species alter the soil communities, causing an increase in pathogens and thus, indirectly influencing native species. While the accumulation of local pathogens may limit the invaders abundance, it may hit the native plant community more negatively. Following extensive studies, this hypothesis may explain the success of the invasion of marram grass in California and the resulting exclusion of the native dune-mat plant community (Eppinga et al., 2006).

When a species invasion occurs, the non-native species may also benefit from

parasite spillback (Kelly et al., 2009). This occurs when the non-indigenous invader is a competent host for a native parasite. The invader can become infected with this parasite which can then spill back to the native species, thus increasing the disease impact on the native species. An example of spillback is the population decline of the native grape leaf hopper (*Erythroneura elegantula*) in California as the invasive variegated leaf hopper (*Erythroneura variabilis*) has spread. The eggs of both species are naturally parasitised by the hymenopteran *Anagrus epos* which kills its host upon emergence. This parasitoid usually prevents grape leaf hoppers from damaging crops too severely. The variegated leaf hopper is less susceptible to parasitoidism than the native species, leading to increased parasitoidism of the grape leaf hopper and thus, its decline (Strauss et al., 2012).

Disease can also facilitate an invasion when an infectious parasite is brought with the invader. Typically, when the disease has reached a high prevalence, it may spill over to infect the susceptible native competitors, thus increasing the invaders chance of establishing in the area successfully (Power and Mitchell, 2004). As any non-indigenous individuals infected with virulent parasites are likely to have died during translocation, it is likely that these parasites will have minimal effects on their original hosts, the invading species (Strauss et al., 2012; Dunn and Hatcher, 2015). However, they have the potential to cause virulent diseases in native species which are unlikely to have been exposed to such parasites before. Thus, the non-indigenous species can become a reservoir for diseases that can cause high mortality to native species. This is termed “spillover disease-mediated invasion” (DMI) (Strauss et al., 2012). Of particular concern is the fact the parasites causing the diseases are non-indigenous species themselves. This indirect enemy alliance is an example of invasional meltdown leading to the outbreak of disease at the same time as the invasion of a species (Strauss et al., 2012).

There are examples of disease-mediated invasion aiding human expansions across the globe. For instance, in 1520 smallpox arrived in Mexico with one infected slave arriving from Spanish Cuba. The resulting epidemic is thought to have killed roughly half of the Aztec empire, including an emperor. This strange illness puzzled and demoralized Aztec survivors as it killed Indians while sparing the already immune Spaniards. By 1618, Mexico’s initial population of 20 million had fallen to approximately 1.6 million. The Native American populations of the United States suffered severe impacts from disease which advanced ahead of European explorers. Therefore, as the Europeans spread across the land, there was significantly reduced resistance from native communities as they had all been wiped out due to disease induced mortality. Disease was clearly a biological weapon mediating the European invasion of the Americas (Diamond, 2005).

Disease-mediated invasion also has a large impact in wildlife populations. For

example, local population extinctions and widespread decline of the native white clawed crayfish (*Austropotamobius pallipes*) are thought to be due to spillover of the fungus *Aphanomyces astaci* from the invasive signal crayfish (*Pacifastacus leniusculus*) across Europe following the release/escape and consequent establishment of the signal crayfish (Dunn and Hatcher, 2015). The emerging pathogenic fungus *Batrachochytrium dendrobatidis* that causes chytridiomycosis infection in amphibians has been linked to numerous species declines and extinctions across the American continent, Australia and Europe (Berger et al., 1998; Garner et al., 2006; Bosch et al., 2001). The spread of the fungus is thought to be aided by the American bullfrog (*Rana catesbeiana*). The bullfrog, which shows low mortality to the infection (Garner et al., 2006; Daszak et al., 2003) and has been introduced across the world, is a likely reservoir of the fungus. A case study example of disease-mediated invasion in the UK is the replacement of red squirrels by grey squirrels which is thought to be enhanced by squirrelpox virus (as well as competition). We will focus on this case study system below.

1.4 Squirrels in the UK

As the temperature increased and forest cover replaced tundra habitats at the end of the last ice age (around 12500-10000 years ago), it is thought that Eurasian red squirrel (Figure 1.1) colonised the British Isles from continental Europe (Shorten, 1954; Bosch and Lurz, 2012). Since then, red squirrel numbers have fluctuated greatly, largely declining as a result of deforestation between the 15th and 16th centuries, with extinction thought to have occurred in Ireland in the 18th century until reintroductions in the 19th century (Scharff, 1922, 1923; Moffat, 1923). Extinction also came close in Scotland in the 18th century when large scale woodland clearances occurred for agriculture, sheep grazing and to be used as fuel. Numbers recovered in Scotland with the aid of reintroductions in 1770-1850 (Shorten, 1954; Bosch and Lurz, 2012). Following extensive afforestation in the British Isles in the 18th and 19th centuries, numbers became so high that they were considered a nuisance in places like Cornwall and the Highlands of Scotland. As a result, “Squirrel Clubs” were set up to shoot squirrels and keep the numbers controlled. Thus, at around the start of the twentieth century, red squirrel populations were flourishing (Shorten, 1954; Bosch and Lurz, 2012).



Figure 1.1: Red squirrel ©Hannah Jones

Towards the end of the nineteenth century, from 1876 -1902, there were a series of introductions of another squirrel species, the North American grey squirrel (Figure 1.2), at various locations in England, including Chester, Middlesex, Bedfordshire and Surrey (Middleton, 1930). Greys from populations that became well established were then translocated to further places such as Yorkshire, Norfolk and Ayrshire (Middleton, 1930). Grey squirrels spread and greatly increased in numbers, after the initial introductions and translocations, although a marked decline in grey numbers was observed in 1932 (Middleton, 1932). The decline was attributed to food shortages due to crop failures in 1930 (Middleton, 1930). By 1935, grey numbers were on the rise again (Middleton, 1935) and continued to increase as they spread further across England and Wales. In the 1940s, they were considered a pest due to bark-stripping damage in forests, but despite the efforts by roughly 7000 squirrel clubs, the population of grey squirrels in the UK continued to rise.

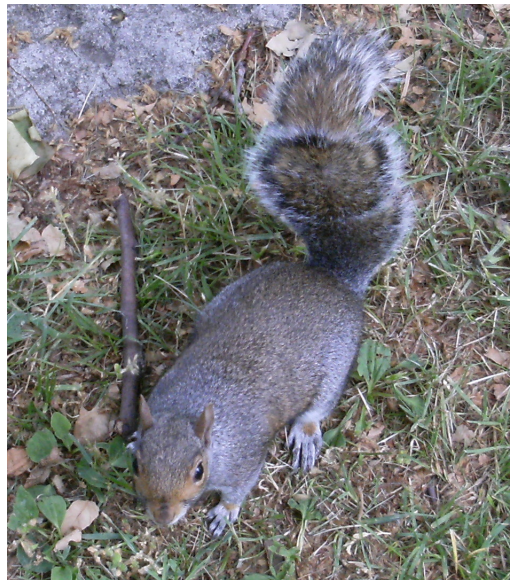


Figure 1.2: North American grey squirrel ©Hannah Jones

The increase in the distribution and density of grey squirrels coincided with a decline in red squirrel distribution (Figure 1.3) and the cause of this severe decline in red squirrel populations has been the subject of much research. Gurnell et al. (2004) reported that there was little evidence of direct aggression from grey squirrels on reds, but the extensive overlap in ecological requirements suggests that interspecific competition for resources between greys and reds may be partly responsible for red decline (Reynolds, 1985; Gurnell et al., 2004). Having evolved with competition from the American fox squirrel, selection has resulted in the grey squirrel having a higher reproduction rate and more versatility with food resources than the red squirrel. While the presence of greys does not affect red adult survival, it does reduce the breeding rate and recruitment of red squirrels (Gurnell et al., 2004). In areas where both grey and red squirrels are present, grey squirrels are found to be better at competing for high energy cached tree seeds at critical times of the year, resulting in a lower fitness of both breeding female red squirrels and young (Gurnell et al., 2004). Both red and grey squirrels can breed twice a year, with litter sizes approximately 2 or 3 per litter and 4 or 5 per litter respectively (Okubo et al., 1989). Furthermore, in the presence of grey squirrels, fewer red squirrels are born and it is thought that young grey squirrels acquire the best habitat patches before red squirrels are able to settle, forcing them into worse habitat (interspecific hierarchy based on body weight) (Gurnell et al., 2004).

While interspecific competition seemed to offer a good explanation for the replacement of red squirrels, observations on the ground showed a more complicated pattern. The well studied replacement of red squirrels by greys in Norfolk in the UK (Reynolds, 1985) indicated that there were areas in which red squirrels appeared

to be dying out before greys established in the area. Furthermore, coexistence occurred for up to 16 years before greys replaced reds in some areas (Reynolds, 1985). At the end of the study in 1982, many areas which had grey squirrel populations, had never previously had red squirrels recorded there, while there were areas that had previously recorded red squirrels that did not contain grey squirrels (Reynolds, 1985). Therefore, no obvious spatial pattern was visible. Thus, although competition between red and grey squirrels could explain some of the replacement of reds in the UK, it did not appear to be the sole reason.

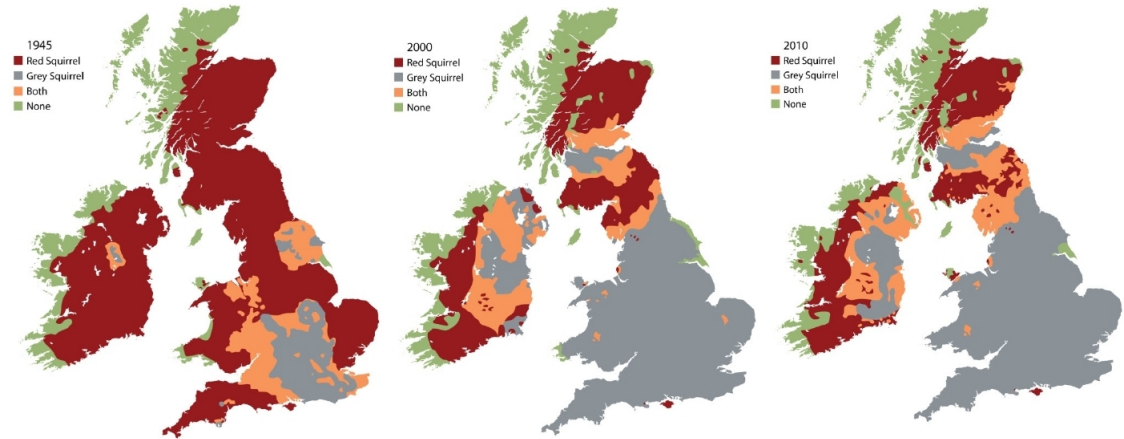


Figure 1.3: Distribution change of squirrels in the Britain and Ireland (Craig Shuttlesworth, 2014).

As competition alone could not account for the pattern of replacement of reds by greys in the UK, alternative mechanisms were considered. Previously epidemics of disease have been observed in red squirrels in parts of the UK, but only on a local scale (McInnes et al., 2016). In 1962, a myxomatosis like disease was reported to wipe out all but one red squirrel in Shropshire in 1960 (Edwards, 1962). The description of the disease matches closely with what we now call squirrelpox virus (SQPV) (McInnes et al., 2006). However, at this time little was known of the disease and it was not until 1984 that the poxvirus (originally thought to be a parapox virus) was isolated from eyelid lesions in a dead red squirrel (Sands et al., 1984). However, grey squirrels were frequently dismissed as the source of the disease as red squirrels appeared to contract the disease in areas outside the current geographical range of the grey squirrel (Reynolds, 1985). Moreover, red squirrels continued to be recorded in Norfolk in areas in which the disease had occurred (Reynolds, 1985). While SQPV was seen to be causing high mortality of reds (Figure 1.4), at this time (c 1985), greys were not thought to be the source of the disease.

It was not until 1996 that a grey squirrel was observed with SQPV and thus,

grey squirrels were directly implicated as potential carriers of the disease in red squirrels (Duff et al., 1996; McInnes et al., 2016). Enzyme-linked immunosorbent assay (ELISA) was developed to look for evidence of the infection in both red and grey squirrels (Sainsbury et al., 2000). A serological survey of red and grey squirrels was conducted to study the patterns of the disease and the possibility that the grey squirrel acts as a reservoir. Extensive testing of serum samples of both red and grey squirrels highly favoured the suggestion that the grey squirrel is a reservoir host as 61% of squirrels tested around the UK had sero-prevalance while only 2.9% of reds were sero-positive (Sainsbury et al., 2000). The low percentage of sero-prevalence in red squirrels suggested that the disease is fatal to the red squirrel while having no adverse consequences on the grey squirrel (Sainsbury et al., 2000). It is thought that grey squirrels have developed a resistance to the disease as it co-evolved with them in the USA (where antibodies to the disease have been observed in grey squirrels (Thomas et al., 2003)). It was also shown in the laboratory that the squirrelpox infection could indeed infect both squirrel species (Tompkins et al., 2002). In Scotland and Ireland, the disease was not found in red squirrels at this time, nor was there any sero-prevalance in grey squirrels. Therefore, there appeared to be a relationship between the geographical distribution of grey squirrels with the antibody to squirrelpox virus and locations where the disease is thought to have occurred (Sainsbury et al., 2000).

As a result of the study of Sainsbury et al (2000), SQPV is considered to be increasingly important in explaining the replacement of red squirrels. As the geographical range of the grey squirrels has expanded, so has the occurrence of the disease in these new grey habitats. The spatial relationship between disease in red squirrels and the sero-positive grey distribution strongly suggests that the grey squirrel is a reservoir of SQPV (Sainsbury et al., 2008).



Figure 1.4: Red squirrel with squirrel pox ©SAGG C Kippax 2007 (Squirrel Action Greenhead & Gilsland, 2007)

The evidence therefore suggests that the transmission of SQPV and the resulting disease in red squirrels seems to have given the grey squirrels an advantage, allowing the grey squirrel to spread and increase in numbers over the past 100 years. In areas with both red and grey squirrel populations and no detected SQPV (Scotland until recently, and currently Italy), the decline in the red squirrel populations has been much slower than in areas with the disease (Sainsbury et al., 2008) but it has taken a long time to make the connection between disease and red replacement. One reason for this is that in general, it is thought that a red squirrel dies within two weeks of infection of the disease. Such a short infection period makes it difficult to observe the disease in red squirrels, so many cases of the disease will not be recorded (Tompkins et al., 2003). As the increasing rate of ecological replacement of reds by greys coincides with disease in reds and the presence of antibodies in greys, while other factors remain unchanged, it is now widely accepted that SQPV is an important factor in red squirrel extinction through a process of disease-mediated invasion.

1.5 Overview of mathematical modelling of the UK squirrel system

The now accepted view that squirrelpox has played a key role in the replacement of red squirrels in the UK resulted from observation and experiments but also from mathematical modelling. Due to the non-linear complexities of ecological systems, such as the disease in the squirrel system, mathematical models are essential to un-

cover the key biological processes that drive the changes to the population dynamics (Strauss et al., 2012).

Mathematical models have been used to study species interactions and population dynamics of ecological systems for many years. In 1926, Lotka and Volterra developed mathematical frameworks to understand dynamics of interacting species (see Murray (2002)). These models could explain key biological processes such as the competitive exclusion and cycles in population abundance as a result of species interactions. Around the same time, Kermack and McKendrick (1927) (later extended by Anderson and May (1979)) began modelling of infectious diseases with a compartmental model that separated the host into Susceptible, Infected or Recovered classes (the SIR model) to describe the population dynamics of infectious disease (see Murray (2002)). A key result outlined the concept of the basic reproductive ratio of the disease, R_0 . When $R_0 > 1$, the disease can persist in the population. While being a greatly simplified representation of the real world, these model structures are the foundations of many of the more recent, sophisticated models that aim to include additional biological realism to answer current questions in ecology. In particular, they have been a crucial tool for understanding the complex interactions of competition, disease and landscape features in the replacement of red by grey squirrels in the UK.

The first significant mathematical model of the red and grey squirrel system in the UK was developed by Okubo et al. (1989). The Lotka-Volterra competition framework was extended to include the spatial dispersal of squirrels by including a diffusion term to represent random movement. They parameterised the model from life history data and assumed that grey squirrels have a competitive advantage over reds. Their aim was to show that competitive pressure from greys could lead to the observed expansion in the distribution of greys and replacement of reds. Their work showed that a travelling (invasion) wave would spread from the point of grey squirrel introduction, transforming red squirrel populations behind the wave. A detailed comparison with observed red replacement was not presented, due largely to lack of available data, but Okubo et al. (1989) concluded that a general form of competition was sufficient to account for the progressive replacement of red by grey squirrels in England and Wales.

Rushton et al. (1997) developed an alternative approach for modelling red and grey squirrel competition. They created individual based models to represent reproduction, mortality, competition and dispersal of red and grey squirrels in a realistic habitat (obtained through Geographical Information Systems (GIS) analysis of satellite landcover data and forestry records). The population processes in this framework are modelled using rule-based algorithms. This spatially explicit population modelling (SEPM) links deterministic models of life history processes with the

spatial distribution of the habitats squirrels are found in. Therefore, considerable complexity can be included in the model, with rules representing detailed behaviours and life-history scenarios with varying adult and juvenile mortality rates, fecundity, habitat carrying capacity and maximum dispersal distances. While such models can predict the distribution of squirrels in the landscapes for which they were developed, it is difficult to isolate the important facts influencing the population dynamics due to the complexity of the rules and the large number of parameters included. They compared the model findings with the observed replacement of reds by greys in Norfolk, East Anglia between 1960 and 1981 (Reynolds, 1985). The model predicted the competitive replacement of reds, but the closest fit to the observed expansion of grey squirrels and decline in reds required that mortality was lower and fecundity higher in grey squirrels than that obtained from field estimates. This led to an extension of the rule-based modelling framework to additionally include the impact of squirrelpox virus. The model results were again compared to the findings of Reynolds (1985). Rushton et al. (2000) concluded that SQPV, like interspecific competition, could have led to the replacement of reds in Norfolk. Combining both disease and competition barely altered the predicted rate of decline in red squirrel populations. All predictions appear to be independent of whether competition, disease or competition and disease are modelled. Due to the complexity of the rule-based systems, the key driving factors in the population behaviour cannot be seen. This modelling approach has also been used to successfully predict the expansion of grey squirrels in North Italy (Lurz et al., 2001), to assist in the development of landscape-scale conservation strategies in the North of England (Lurz et al., 2003; Gurnell et al., 2006) and has been extended to understand the population dynamics of a range of squirrel species (Rushton et al. (2006) and see Lurz et al. (2008) for a review).

The data of Reynolds (1985) on the replacement of red squirrels in Norfolk was also the focus of a modelling study by Tompkins et al. (2003), who combined the classical deterministic techniques for modelling competition (as in Okubo et al. (1989)) and infectious disease (Anderson and May, 1979), to assess the impact of disease-mediated invasion. Tompkins et al. (2003) used a simplified representation of habitat where carrying capacity was the same in each of an array of 5km by 5km gridsquares. They showed how simulation with competition alone could not replicate the replacement of reds by greys observed in the field, but that including SQPV in addition to competition was essential for the model results to match observations. The model provided an intuitive biological explanation for the enhanced replacement and showed that SQPV induces an epidemic in red squirrels that greatly reduces their density, and invading greys can therefore replace reds more rapidly. Furthermore, the model showed that although SQPV is a key driver of red replacement, the density of infected individuals at any time is low (due to the high virulence of

SQPV in reds) and therefore would be difficult to observe in the field. Tompkins et al. (2003) emphasised that the role of pathogens must be considered when assessing the impact of species introductions and that mathematical models could be extended to understand specific questions in the ecology and conservation biology of the UK squirrels system.

The deterministic approach of Tompkins et al. (2003) provides a clear understanding of influential mechanisms that arise between interacting populations that share a disease, but cannot accurately assess the risk of invasion of grey squirrels or SQPV spread as they do not include the chance of extinction or disease fade-out at low density that may arise through stochasticity. As initial invasions and infection levels are at a low density, this is very significant in DMI modelling. Given Tompkins et al. (2003) is a deterministic model, it may support very low densities of infecteds which in reality would have died out. The rule-based approaches of Rushton et al. (1997, 2000, 2006) include stochasticity, but here it is difficult to determine the key drivers of the population dynamics due to the complicated arrangement of rules and large number of model parameters. Important system-specific life history properties such as seasonality and age structure have been found to be key drivers in population change in single host-parasite systems (Strauss et al., 2012) so their role in shared disease systems must be investigated and incorporated into the model when necessary.

To answer specific issues regarding the conservation of UK red squirrels, White et al. (2014) considered a framework that lay between the two previous approaches. They developed a stochastic version of the model of Tompkins et al. (2003) and used it to assess the importance of grey competition and SQPV in forests managed for red squirrel conservation (strongholds). Strongholds are local forest regions that are large enough to sustain viable red squirrel populations over the long-term, and in which habitat composition and management offers native red squirrels a competitive advantage over greys. White et al. (2014) indicated that in regions where grey squirrels have a competitive advantage over reds, control was required to prevent grey invasion and protect red populations within the stronghold. A key result indicated that SQPV spread from adjacent grey populations could lead to epidemic outbreaks in reds in the stronghold even when the invading species is prevented from establishing. The model predicted that there would be periodic SQPV epidemics that lead to a population crash in reds in the stronghold, followed by disease fade-out and the recovery of reds to pre-infection levels. The model predictions are supported by evidence from UK red squirrel strongholds in Formby and Whinfell, where reds are protected by trapping and removal of greys but have suffered repeated outbreaks of SQPV (Parrott et al., 2009).

The stochastic framework of White et al. (2014) provided a clear understanding

of the role of disease in conservation strongholds, however the spatial set-up was idealised. In White et al. (2016a), the framework of White et al. (2014) was extended to examine the red-grey-SQPV system on a realistic landscape that includes habitat information extracted from digitised landcover maps using GIS (see also White and Lurz (2014)). This was used to study the effects of control on the Fleet Basin red squirrel stronghold, Dumfries and Galloway (White et al., 2016a) and the spread of squirrelpox through southern Scotland (White et al., 2016b).

In this thesis we extended this model to include seasonality and use it to investigate squirrel population change in various areas in the UK in relation to management and disease. Firstly, in Chapter 2 we consider the red squirrel stronghold sites of Kidland and Uswayford forests. Here we consider the effects different felling and re-planting strategies have on red squirrel viability. In Chapters 3 and 4 we model the past and present squirrel populations on the Isle of Anglesey and in the surrounding area. In Chapter 3, we examine the influence of squirrelpox in the replacement of red squirrels on Anglesey. Chapter 4 builds on this to include the control of grey squirrels in the model and uses the model to determine the best strategies to maintain the red squirrel stronghold on Anglesey. Strategies to expand the red squirrel stronghold are also considered. Finally, in Chapter 5 we revisit one of the key theoretical results on disease-mediated invasion in which deterministic models show that a wave of disease can spread ahead of a wave of invasion. We examine whether this results holds in stochastic models and the implications for disease-mediated invasion in natural systems. Therefore, the key aim of this thesis is to use mathematical modelling to direct strategies to conserve the remaining populations of red squirrels in the UK and to more generally understand the processes of disease-mediated invasion, and its potential impact on ecological replacements.

Chapter 2

Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel

This chapter is based on the peer reviewed manuscript:

Jones H, White A, Geddes N, Clavey P, Farries J, Boots M, Lurz P (2016) Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel, *Hystrix*, *The Italian Journal of Zoology*, 21, 1

The chapter is presented as the published version of the paper. I did all of the mathematical modelling. Peter, Andy and I wrote the paper together. In addition we have enhanced the paper by citing supporting information and additional results that are presented in an appendix at the end of the chapter.

2.1 Abstract

The Eurasian red squirrel (*Sciurus vulgaris*) is under threat in the UK from the introduced North American grey squirrel (*Sciurus carolinensis*). National measures to save the species include large conifer forest reserves where management encompasses measures to bolster the native species. However, forests are multi-purpose environments and foresters have to balance different timber production, amenity and conservation objectives. We present a mathematical modelling framework that examines the impacts of potential felling and restocking plans for two reserves, Kidland and Uswayford forests, in northern England. In collaboration with forest managers, we employed an iterative process that used the model to assess four forest design plans (felling and restocking scenarios) with the aim of improving red squirrel pop-

ulation viability. Overall, the model predicted that extinction in both forests at the same time was rare, but high in Uswayford (84%) alone. Survival could be drastically increased (from 16 - 70%) by felling and restocking adjustments, and improving dispersal between the two adjacent forests. This study provides an exemplar of how modelling can have a direct input to land management to help managers objectively balance the differing pressures of multi-purpose forestry.

2.2 Introduction

The management of forest systems will face a range of challenges in the coming decades as a result of global climate change, emerging tree diseases and a need to integrate forest ecosystem services such as timber extraction or amenity with efforts to preserve biodiversity (Bengtsson et al., 2000; Brown and Webber, 2008; Ray, 2008; Ray et al., 2010; DEFRA, 2011; Shuttleworth et al., 2012). Mathematical modelling can play an important role in helping to address these challenges. In particular, models that are combined with digital landcover data and knowledge of species habitat requirements and behaviour form powerful and highly successful tools for species conservation and management. Examples of modelling approaches that combine mathematical models and spatial data include GIS-based landcover mapping approaches linked with simple models to predict future land development impacts on deer (*Odocoileus hemionus*; Kline et al. (2010)); using spatially explicit population models to assess the potential success of species translocations for butterflies (*Maniola jurtina*, Heikkinen et al. (2015); the development of a spatially explicit agent-based model to simulate tiger (*Panthera tigris*) population and territory dynamics (Carter et al., 2015); or the use of spatial, stochastic models to study the impact of disease-mediated competition by the introduced North American grey squirrels on Eurasian red squirrels (White et al., 2014).

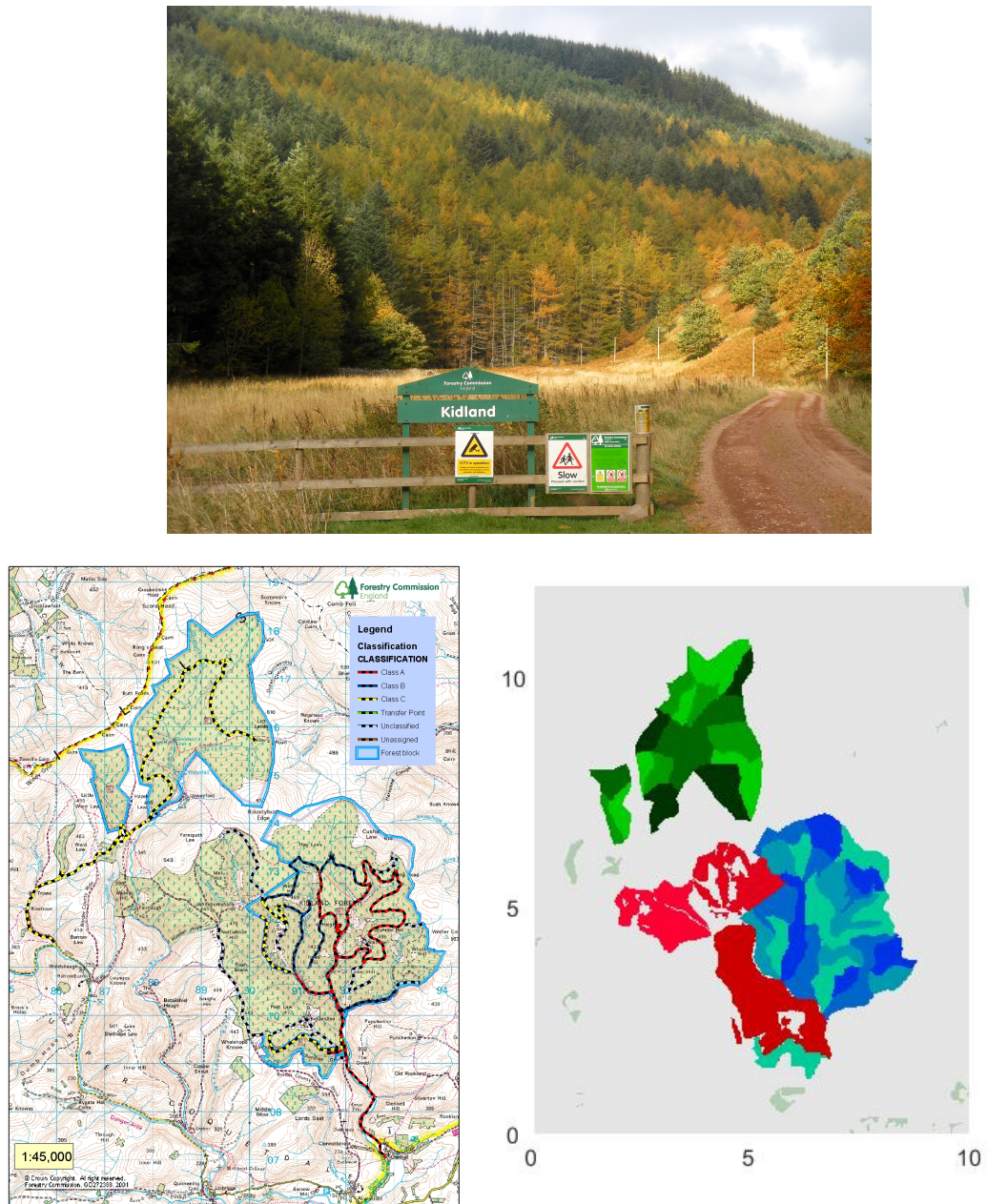


Figure 2.1: (top) A photograph of Kidland forest highlighting how it is dominated by conifer (©Peter Lurz). (left) The Forestry Commission relief map of Kidland and Uswayford forests and (right) the representation of compartments in the model with the Kidland compartments (blue), Uswayford (green) and Private (red).

A key benefit of models is their ability to pose “what if” questions that assess the likely effects of future land use changes or species management. Their use allows objective assessments of different management options and can assist in developing the most effective conservation strategies. Here we present the application of a spatially explicit, stochastic population dynamics model that was used to evaluate the likely impacts of different forest design scenarios on the population persistence of Eurasian red squirrels, a species under threat of extinction in the UK (Gurnell

et al., 2004; Lurz et al., 2005). In close collaboration with the Forestry Commission, the government forestry organisation in the UK, we examined the future felling and restocking scenarios for Kidland and Uswayford forests (Fig. 2.1), two spruce-dominated, conifer woodlands in the north-east of England (Figure 2.A.1). The two forests are part of a network of 17 English conifer-dominated strongholds for the endangered red squirrel, where favourable habitat and management aims to reduce the competitive and disease impacts of invading grey squirrel populations (grey squirrels carry squirrelpox virus that is lethal to red squirrels; (Tompkins et al., 2003)) and thus ensure long term survival of local red squirrel populations (Parrott et al., 2009; Anonymous, 2012).

A large number of forests (38% of the UK forest area) are managed by the Forestry Commission, and the Forestry Commission is a key partner in the efforts to save red squirrels in Britain. With respect to the north of England, they manage a significant or majority proportion of the seven red squirrel reserves, all of which are forests planted in the 20th century. Whilst the forests were initially established to provide a strategic timber resource, there are now multi-purpose management objectives that balance timber production with recreation and conservation. The whole of Uswayford forest and approximately half of Kidland forest is owned and managed by the Forestry Commission. The remainder of Kidland is in the hands of a number of private owners. The two forests are composed predominantly of Sitka spruce (*Picea sitchensis*) as well as a small proportion of other conifer species. They were planted on open moorland and red squirrels colonised during the last century. They are relatively isolated and therefore the likelihood of invasion by grey squirrels is low.

Monitoring for red squirrels at Kidland forest has occurred for the last 15 years on an annual basis. The forest habitat supports low density populations of red squirrels and is thought to be unfavourable for greys. A key determinant of red squirrel abundance in these regions is resource availability which will depend on the availability of mature seed producing trees suitable for red squirrels (which in turn varies depending on felling and restocking strategies) and seed crop abundance (which varies annually due to climate patterns, weather and phenology), (Bosch and Lurz, 2012). The close association of red and grey squirrels with forest habitats and their maturity make them ideal species for assessment with models (Lurz et al., 2001, 2003, 2008). Linking mathematical models with digital landcover maps, or the highly detailed UK forest stock maps which provide information on tree species (planted as single species blocks) and age classes (planting year) at high resolutions, allows accurate simulations of different forest management options.

In this study we use mathematical models and digital landcover maps to assess how red squirrel abundance would change as a result of different forest design plans.

The objective was to use an iterative process where modelling that assesses whether red squirrel population dynamics can inform the development of further forest design plans, with the aim of ensuring and improving red squirrel viability. This iterative process led to the consideration of four different forest design plans (scenarios A - D outlined in the methods sections) in which the model predicted squirrel densities as Kidland and Uswayford are felled and replanted. The model study outlines the scenarios that are most favourable for red squirrel abundance and viability and this information has been used by the Forestry Commission in the production of the proposed forest design plans for these regions.

2.3 Methods

2.3.1 Study Area

Kidland and Uswayford are part of the North England Forest District, in Northumberland, England. They were planted post 1960 and are commercially managed. Kidland is 2050 ha, of which 1190 ha are managed by the Forestry Commission, the rest is owned by private landowners managed by the company Tilhill; while Uswayford is approximately 1000 ha, all managed by the Forestry Commission. The two forests are separated by less than 1 km of open land (Figure 2.1), but are relatively isolated from other forested regions and surrounded by moorland. They are dominated by conifer species such as Sitka spruce, Norway spruce (*P. abies*), Scots pine (*Pinus sylvestris*), Lodgepole pine (*P. contorta*) and larch, (*Larix* spp.; see also Figure 2.1). Using Forestry Commission data, we extracted the compartments that represent Kidland and Uswayford (see blue and green regions respectively in Figure 2.1c) and the privately managed Tilhill area on the western side of Kidland (see red region in Figure 2.1c).

2.3.2 Carrying capacity estimate

The number of squirrels that the different forest compartments can support depends on habitat type, which can be estimated using Forestry Commission stockmap data (or publicly available forest inventory records for private areas). This data provides species specific habitat and age information within each compartment which can be combined with squirrel density estimates from the literature and data from the existing 15 years of local squirrel and tree seed crop survey data (Forestry Commission pers. comm.; Table 2.1). It is assumed that it takes 30 years for trees to reach maturity and provide suitable, regular resources (seeds) for red squirrels. As felling plans for the adjacent, privately managed forest area were not known in detail, the

land was taken to be one third felled, one third immature and one third mature, which replicates a 45 year conifer rotation cycle typical for upland conifer plantations. This also kept private forest areas neutral and allowed the project to focus on assessing the impacts of any proposed Forestry Commission design plans only, without confounding the results with changes to the structure of adjacent woodland. We determined a high and low carrying capacity to reflect good and poor seed years for each compartment using published density estimates, taken from the following references: Holm (1991); Magris (1998); Lurz et al. (1995, 1998); Bosch and Lurz (2012); White et al. (2014). The estimated red squirrel densities per hectare for each tree species class is shown in Table 2.1, and Figure 2.2 shows the resulting high and low carrying capacities for the forests in 2012.

Red Squirrel Density (/ha)		
Tree Species	High	Low
Ash	0	0
Birch	0	0
Douglas fir	0.45	0.17
European larch	0.38	0.21
Grand fir	0	0
Hybrid larch	0.38	0.21
Japanese larch	0.38	0.21
Lodgepole pine	0.4	0.04
Mixed broadleaf	1	0.62
Norway spruce	0.58	0.25
Oak	1	0.62
Scots pine	0.4	0.04
Sitka spruce	0.11	0.011
Sycamore	0	0
Western hemlock	0	0
Other conifer	0.45	0.17
Other spruce	0.2	0.02
Mixed conifer	0.45	0.17

Table 2.1: Estimated red squirrel carrying capacities. The data was derived from a variety of references, see Bosch and Lurz (2012); Holm (1991); Lurz et al. (1995, 1998); Magris (1998); White and Lurz (2014)

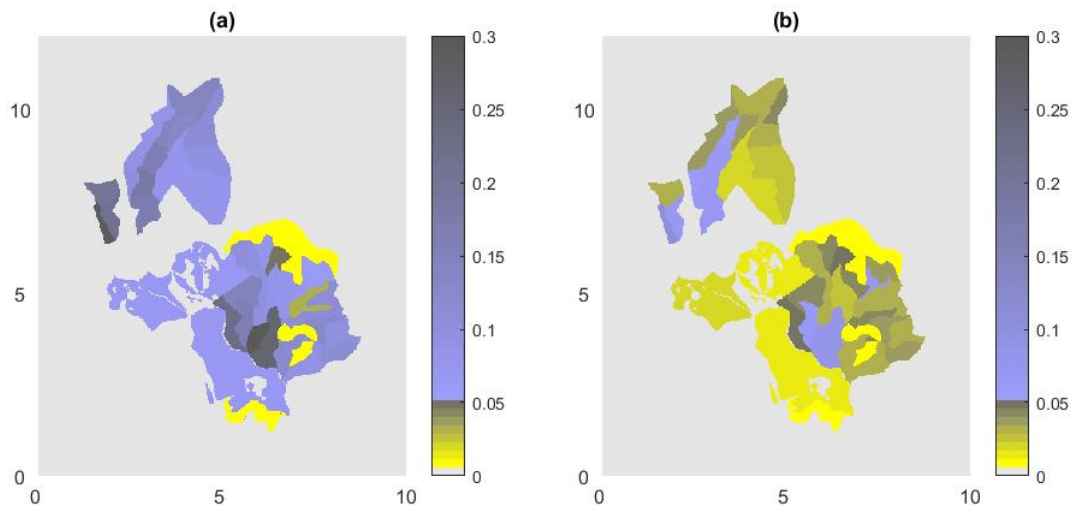


Figure 2.2: Red squirrel carrying capacity estimates for Kidland, Uswayford and Tilhill in 2012. (a) The high estimate (Table 2.1) representing a good seed year and (b) the low estimate (Table 2.1) representing a poor seed year.

2.3.3 Forest Design Plans (Scenarios A-D)

The initial forest design plan (named scenario A) supplied by the Forestry Commission contains felling and species specific restocking information from 2012-2052. This was created prior to the modelling assessment and was based on commercial considerations without a focus on red squirrel conservation. The felling and restocking information in scenario A can be used to produce carrying capacity maps for each year between 2012-2052 (shown for every two years in Figures 2.A.2 and 2.A.3). The initial model predictions using scenario A were presented to the Forestry Commission in May 2014 and led to the development of three further scenarios (B, C, D) that attempted to improve red squirrel population viability while taking into account local planting and felling constraints (e.g. restrictions due to tree diseases and wind throw risks for exposed locations). We outline these scenarios below (see Table 2.2 for a summary).

Scenario	Date received	Summary
A	24/2/14	Original forest design plans
B	14/10/14	Updated plans to improve potential density in Uswayford
C	17/11/14	Updated plans with a reduced felling rate in Kidland
D	12/2/15	Economical restocking with delayed felling as in Scenario C

Table 2.2: A summary of the four forest design plans

Scenario B considers an alternative felling plan which extended the time before

some coupes were felled in Uswayford. This aimed to prevent sustained low densities in Uswayford. To compensate, some additional felling was undertaken in Kidland. Carrying capacity maps using scenario B are shown in Figures 2.A.4 and 2.A.5. Scenario C has a similar felling trend to scenario B in Uswayford, but has a reduced rate of felling in Kidland. In addition, the tree species mixture chosen for restocking contains tree species that support a higher density of squirrels (carrying capacity maps using scenario C are shown in Figures 2.A.6 and 2.A.7). Scenario D follows a similar trend to scenario C but the tree species chosen for restocking are chosen based on commercial priorities rather than squirrel habitat quality. They therefore do not support such a high squirrel density as scenario C (carrying capacity maps using scenario D are shown in Figures 2.A.8 and 2.A.9). Figure 2.3 shows the effect of the four different forest design scenarios on the overall carrying capacity of Kidland and Uswayford. In addition to the new forest design scenarios (B-D), the Forestry Commission also provided details of a potential habitat link between the forests (see Figure 2.A.10). In the model runs we therefore considered two possibilities: (i) squirrels cannot utilise the dispersal compartment until 2045 (30 years after planting when trees are assumed to be mature) and; (ii) squirrels can utilise the compartment in 2025 (while the trees may not be suitable habitat for red squirrels after 10 years, they would provide cover for squirrels moving between Kidland and Uswayford).

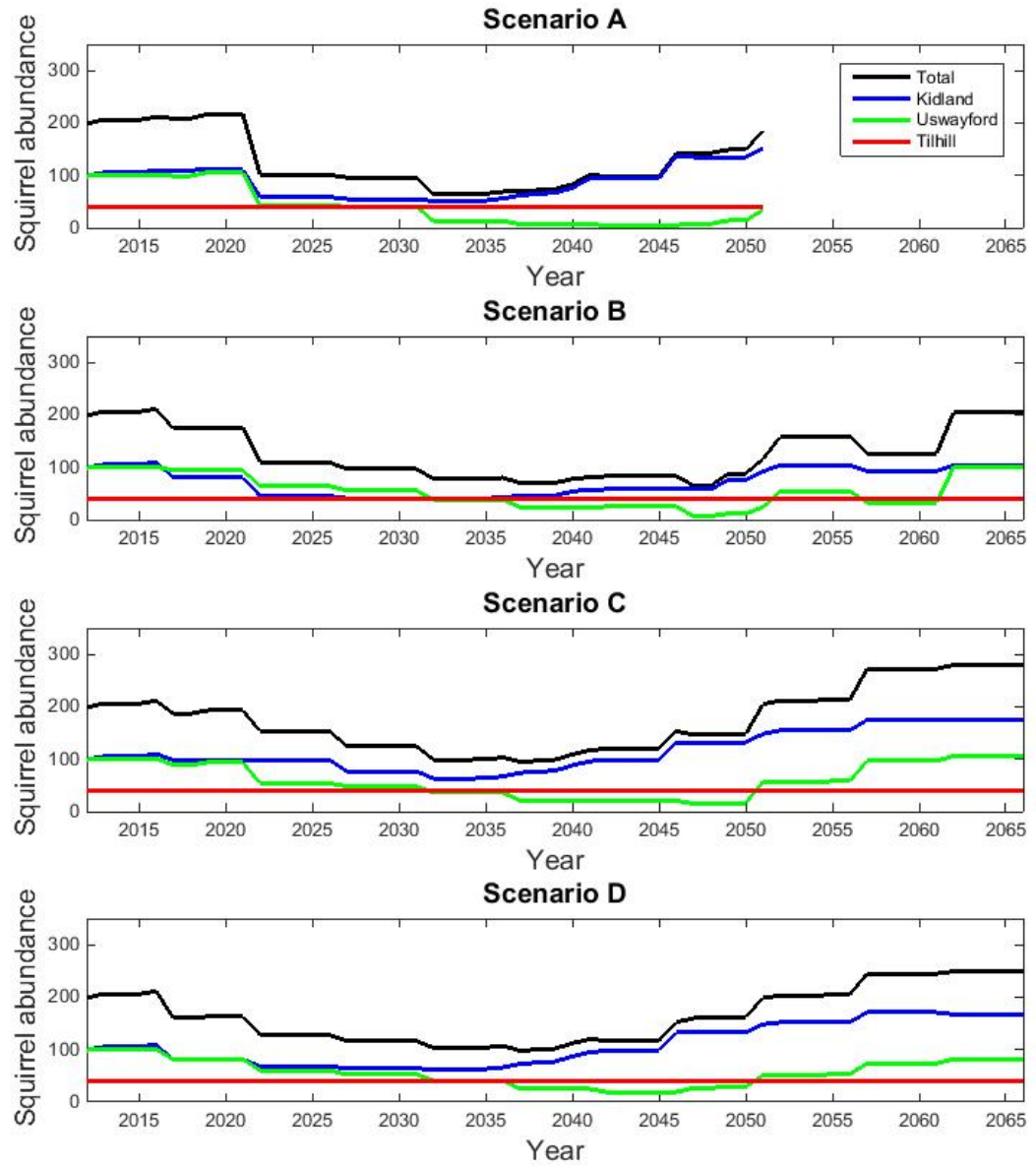


Figure 2.3: Changes in red squirrel carrying capacity using the high density estimates between 2012-2052 for scenario A and between 2012-2066 for scenarios B-D (summarised in Table 2.2). These scenarios were provided as an iterative process in response to model findings with scenario A provided on 24/2/14, scenario B on 14/10/14, scenario C on 17/11/14 and scenario D on 12/5/15.

2.4 Model framework and setup

Previous model studies that have assessed the population dynamics of red squirrels in realistic landscapes have adapted the classical deterministic modelling approach of Tompkins et al. (2003) to consider a stochastic model framework (White et al., 2014; Macpherson et al., 2016a; White et al., 2016b). In the current study it is important to consider the stochastic nature of the population dynamics as population abundance can reach low levels, which could result in regional population extinction. We therefore follow a similar approach to White et al. (2014) in this study. Within each forest compartment the population density of red squirrels, N , at time t , in years, is represented by the following underlying deterministic model:

$$\frac{dN}{dt} = aN \left(1 - \frac{N}{K_1}\right) - bN \left(\frac{N}{K}\right) \quad t_n \leq t < t_{n+1} + 0.5 \quad (2.1)$$

$$\frac{dN}{dt} = -bN \left(\frac{N}{K}\right) \quad t_n + 0.5 \leq t < t_{n+1} \quad (2.2)$$

Here, we assume birth and death are density dependent and that birth only occurs for a 6 month breeding season (representing 2 litter periods between May-October) whereas death can occur throughout the year. The natural mortality rate is $b = 0.9yr^{-1}$ (Barkalow et al., 1970) and the birth rate is $a = 3.0yr^{-1}$ (Tompkins et al., 2003). The carrying capacity, K , is determined using Forestry Commission data for each compartment (see Figure 2.2 and Figures 2.A.2-2.A.9) and the density dependent parameter that scales the birth rate, $K_1 = 2.6K$ is calculated to ensure that the average population density over a year is equal to the carrying capacity, K .

The deterministic model is turned into an individual based stochastic model by turning the rates for births and deaths in Equations 2.1 and 2.2 into probabilities of a birth or death “event”. We also need to consider the dispersal of individuals. We assume saturation dispersal such that individuals are more likely to disperse as the local population increases (Poethke and Hovestadt, 2002). In our models we specify that individuals disperse randomly up to a distance of 1 km and therefore could move to any compartment that is within this distance. We assume the dispersal rate, $m=b$, so that on average squirrels are predicted to disperse to a new compartment once in their lifetime. The spatial stochastic model is shown in Table 2.3.

Event	Outcome	Probability
Birth (breeding season)	$N \rightarrow N + 1$	$[aN(1 - N/K_1)]/R$
Death	$N \rightarrow N - 1$	$[bN(N/K)]/R$
Dispersal	$N_i \rightarrow N_i - 1, N_j \rightarrow N_j + 1$	$[m(N/K)^2]/R$

Table 2.3: Possible events and their outcomes in a particular compartment i , with dispersal occurring to compartment j . The rates from Equations 2.1 and 2.2 are turned into probabilities by dividing by $R = \sum [\text{rates}]$.

We use a Gillespie algorithm (Gillespie, 1977) to select each event and update the number of individuals (and therefore the probabilities) after each event. The time between each event is given by $dt = -\ln(z)$ where z is a uniform random number between 0 and 1 (which assumes the next event is an exponentially distributed random variable; Renshaw (1991)).

Using scenario A, the model outlined in Table 2.3 was run for 100 years with the high and low carrying capacity estimates (Figure 2.2) to represent a spin-up period (see also Figures 2.A.11 and 2.A.12). In order to reflect the natural, annual variation in resources caused by good and poor seed years (e.g. Lurz (2015)), the model is also run for a scenario in which 3 years of the high carrying capacity were followed by 1 year at the low carrying capacity (3 high, 1 low scenario; Figure 2.A.13).

Following the 100 year spin up period, 50 realisations of the model were run for a further 40 years (2012 - 2052), with the carrying capacity being updated yearly depending on the felling and replanting strategy of the scenario A forest design plan. Similarly, 50 realisations of the model were run for a further 55 years (2012-2066) updating the carrying capacity yearly depending on the strategies given in scenarios B - D.

2.5 Results

The spin up period showed that in the high scenario, the red squirrel population can be supported in the long term with an average of approximately 150 squirrels (Figure 2.A.11). In the low scenario, population extinction is predicted in all model runs (commonly within 5-20 years, Figure 2.A.12), indicating that the red squirrel population could not persist if there were only poor seed crop years. In the 3 high, 1 low scenario, the red population can be supported in the long-term (Figure 2.A.13). This scenario also reflects the variation in annual squirrel abundance that is reported in these forest strongholds (Forestry Commission pers. comm.) with abundance peaking at around 150 squirrels after successive good years and dropping to around 35 individuals in poor years. Since the annual variation in resources is a feature of

the natural system the remaining results in this study are presented for the 3 high, 1 low scenario.

2.5.1 Scenario A

The model was run from 2012-2052 using the forest design plans outlined for scenario A and following the 3 high, 1 low seed crop scenario. Complete extinction of red squirrels in both Kidland and Uswayford was observed in 2% of the realisations (Figure 2.4a). However, red squirrel extinction (by 2052) was predicted in Uswayford (only) in 84% of the realisations. When an additional 20 years was simulated beyond 2052 (Figure 2.4a), the red squirrel population at Kidland stabilized, as the replanted forest compartments had matured and could support additional squirrels. However, there was minimal recovery of squirrel numbers in Uswayford. The model runs indicate that Uswayford was not recolonised by squirrels dispersing from Kidland, even though suitable habitat to support squirrel populations in Uswayford was available from 2050 onwards.

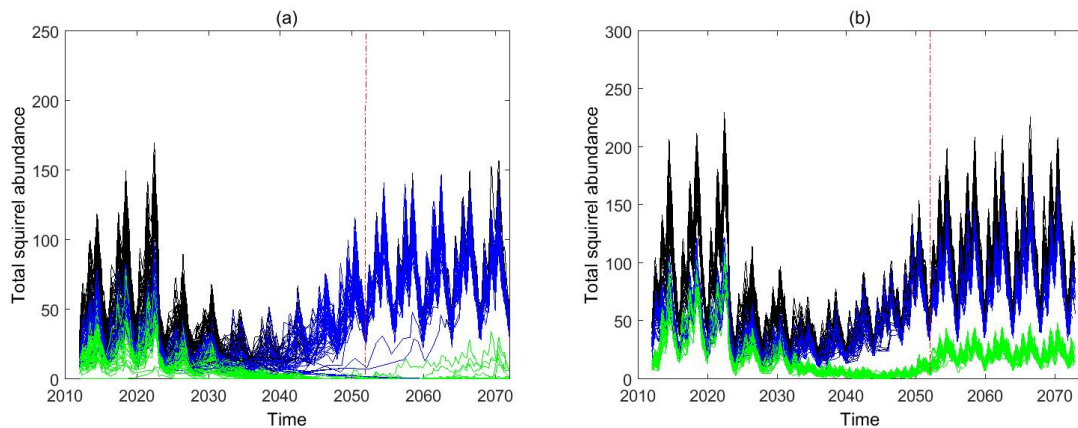


Figure 2.4: (a) The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the ‘3 high, 1 low’ carrying capacity scenario using the scenario A forest design plan for 2012-2052. The model was continued for an additional 20 years at the 2052 levels (highlighted by the dashed red line). (b) The same scenario as (a) with global dispersal (rather than the restriction of 1km to dispersal).

In order to investigate why dispersal from the red squirrel population in Kidland (incl. privately managed Tilhill areas) did not aid the repopulation of Uswayford in the model, we examined the distribution of mature seed-bearing habitat for red squirrels under the forest design plans of scenario A (see Figure 2.A.14). This indicated that there was little suitable habitat in Uswayford between 2038 and

2048 which results in the high levels of population extinction. From 2050 onwards suitable habitat was available in Uswayford, but only a small fraction of this was within the 1 km dispersal distance to the populations at Kidland. Therefore, while some compartment boundaries between Uswayford and Kidland/Tilhill are within the dispersal range for squirrels, felling and replanting meant that the occurrence of mature habitat within the dispersal range was limited.

To explore whether dispersal was a critical factor in the survival or recovery of squirrel populations at Uswayford, we therefore considered an idealised scenario in which dispersal was allowed to any compartment, independent of its location or distance. Figure 2.4b shows that the population abundance still drops to low levels between 2040-2050 due to the low carrying capacity in Uswayford. However, the improved connectivity allows the population to recover in all model realisations. Therefore, recolonisation of Uswayford is hindered by a lack of dispersal opportunities, and a better connection between Uswayford and Kidland/Tilhill would improve recovery in Uswayford following population decline (or extinction) once mature habitat becomes available again. The same investigation was conducted for the high carrying capacity scenario. Details are given in the supplementary information, Figure 2.A.15.

These interim findings were presented to the Forestry Commission in May 2014. It was clear that the planned felling and restocking under scenario A could cause a large drop in the carrying capacities, and therefore squirrel abundance, in both Kidland and Uswayford at the same time. Based on the modelling assessment, the key recommendations to reduce the likelihood of red squirrel population extinction included:

- adjusting the forest management plans so that low carrying capacities (large areas that are felled and/or plantations of an age that do not yet produce seeds) are out of phase in each forest.
- adjusting the tree mixtures to improve the overall carrying capacity.

Discussions with the Forestry Commission also suggested that the model system could be used to consider the effect of an improved connection between Kidland/Tilhill and Uswayford. This would allow one forest to act as a source of squirrels if temporary extinctions were to occur in the other. The impact of a habitat link between forests (see Figure 2.A.10) was considered for scenarios B-D (see below).

2.5.2 Scenarios B, C and D

The scenario A model predictions suggest that Kidland could generally maintain a continuous squirrel population, while the population in Uswayford would fall to very

low levels, supporting few squirrels until a slight increase by 2052 (Figure 2.3 (top) and Figure 2.4a). The chance of population extinction in Uswayford when realistic seed crop patterns were modelled is high (84%). Scenarios B - D were developed by the Forestry Commission in response to these model findings.

In the absence of a dispersal corridor, model simulations for scenario B (Figure 2.5a) show that red population abundance in Uswayford is predicted to fall by around 2052. However, following 2052 the habitat improves and by 2066, populations are recovering to sustainable levels. There is a 46% chance of extinction in 2052 (compared to 84% for scenario A). The scenario C forest design plan further reduced the felling rate in Kidland and model predictions for this scenario support a larger total population of squirrels throughout the period (Figure 2.5d). While there is still a drop in the abundance of squirrels in Uswayford in 2052, only 30% of model realisations result in extinction in Uswayford. Scenario C would therefore reduce the probability of squirrel extinction compared to both scenarios A and B. The model realisations for scenario D (Figure 2.5g) are very similar to those in scenario C, with a chance of extinction in Uswayford of 30% (the same as in scenario C). The total overall population is slightly lower in scenario D than scenario C as the trees used in restocking do not support as many squirrels.

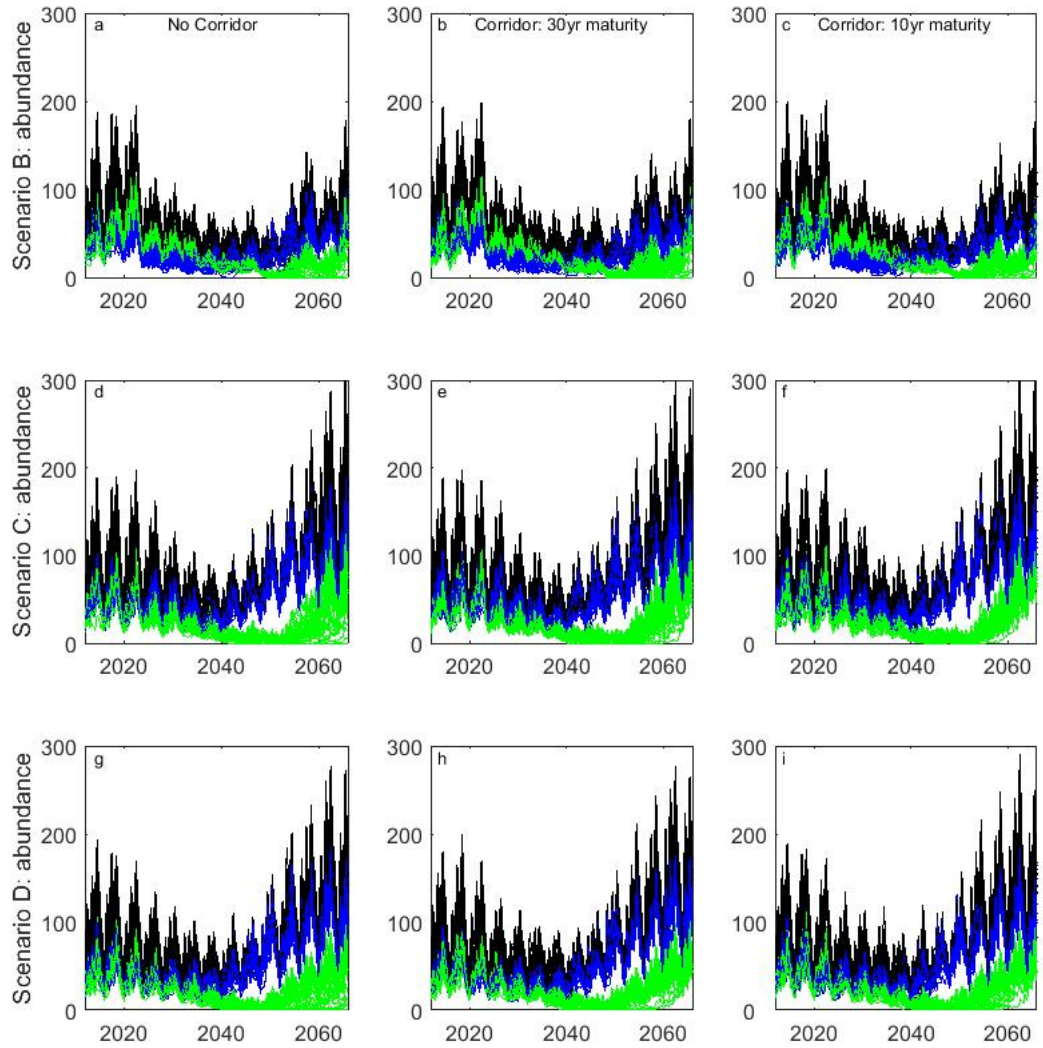


Figure 2.5: The population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black) in the ‘3 high, 1 low’ carrying capacity scenario. (a-c) represent scenario B, (d-f) scenario C and (g-i) scenario D (summarised in Table 2.2). The left column (a,d,g) represent realisations in which the additional dispersal corridor between Tilhill and Uswayford is not included. The middle column (b,e,h) includes the additional dispersal corridor and assumes it can be utilized 30 years after planting. The right column (c,f,i) includes the additional dispersal corridor and assumes that it can be utilized 10 years after planting.

Whilst the new scenarios improve population viability for red squirrels, population abundance still drops to low levels (by around 2050) with a risk of extinction in Uswayford. Population recovery in Uswayford was improved when a dispersal link

was included. Model results indicate that recovery was fastest when the dispersal corridor could be utilised 10 years after planting (Figure 2.5c,f,i). Populations in Uswayford (and the total population) were highest by 2066 in scenario C (Figure 2.5f). To compare the four forest design scenarios (A-D) in more detail, we determined the probability of red squirrels persistence in 2052 under scenario B-D when the additional dispersal corridor between Kidland and Uswayford was included in the model. The chance of total extinction in both Kidland and Uswayford was rare and only occurred in one realisation in the 3 high, 1 low carrying capacity case in scenario A (and in no other model runs). We therefore focus on Uswayford and determine the probability of survival in Uswayford. Without a dispersal corridor between Kidland and Uswayford, the chance of survival is low in scenario A (16%), higher in scenario B (54%) and further increased in scenarios C (70%) and D (70%) (Figure 2.6). Population extinction can still occur in Uswayford when the dispersal corridor is included, but in all of these cases the model predicts improved survival in Uswayford in 2052 (Figure 2.6), and that Uswayford will be re-populated by 2066 (when the corridor is included). Therefore, the dispersal corridor reduces the chance of extinction and significantly improves the re-population of Uswayford if extinction does occur.

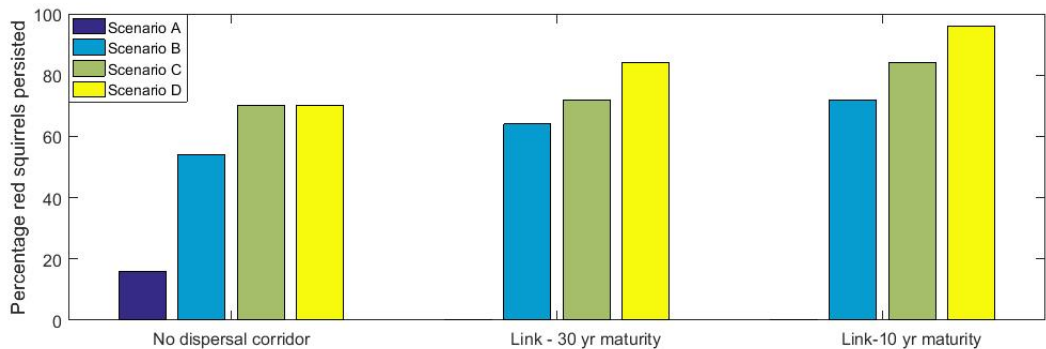


Figure 2.6: The percentage of realisations in which red squirrel populations persisted in Uswayford in 2052 for the four forest design scenarios (summarised in Table 2.2) when there is no dispersal corridor (left) and when the corridor is planted in the compartment shown in Figure 2.A.10 and has a 30 year growth time before it can be used (middle) or a 10 year growth time (right).

2.6 Discussion

Managing forests to improve species conservation and diversity is increasingly important (Hansen et al., 1991; Lindenmayer et al., 1998) but can often conflict with commercial forestry interests which are influenced by economic pressures that may

be detrimental to many species (Ratcliffe and Petty, 1986). Comprehensive and integrated model frameworks can be used to represent ecosystems and their services and to design appropriate methods to handle forest management impacts (Filyushkina et al., 2016). However, efforts to manage forest ecosystem services and preserve endangered species can only succeed when scientists, foresters and landowners work together. Whilst some forest species such as the capercaillie (*Tetrao urogallus*) benefit from intact, mature old-growth forests (e.g. Mikol et al. (2015)), the conservation efforts for red squirrels can be integrated with standard forest operations over the whole woodland area. A high degree of flexibility in red squirrel habitat and space use in conifer forests (Lurz et al., 1995, 1997, 1998, 2000) allows the species to exist at low population densities in production conifer plantations typical of British uplands. These areas offer refuges from the introduced, broadleaf-specialist grey squirrels and form the backbone of current red squirrel conservation efforts in the North of England (Pepper and Patterson, 1998; Parrott et al., 2009). Management for red squirrels in these conifer dominated areas focuses on a few basic recommendations:

- maintaining seed food supply for red squirrels through a minimum level of tree diversity;
- considering forest age structure to ensure there are sufficient mature trees of seed bearing age to support a population;
- maintaining canopy connectivity after thinning and dispersal links within the forest to allow squirrels to resettle as a result of harvesting operations without the risk of predation on open ground (Lurz et al., 2008; Anonymous, 2012; Flaherty et al., 2012).

The permanent retention of small areas capable of supporting a population would also speed up re-colonisation of nearby woodland blocks following harvesting and replanting.

The integration of information on red squirrel population dynamics (Lurz et al., 2005) with local forest management expertise, and mathematical modelling approaches (White et al., 2014) allows assessments of potential impacts of different forest management options on red squirrel abundance. The results of the current study clearly indicate that an iterative, close collaboration can drastically reduce the likely extinction risk for red squirrel populations in Kidland and Uswayford forests and can help in the development of robust conservation strategies. Model findings showed that changes to harvesting and restocking could improve red squirrel viability by ensuring that there was sufficient suitable habitat. Furthermore, an important factor in improved population survival was the consideration of Uswayford

and Kidland as one forest system, realised by the inclusion of a linking, dispersal corridor (see Figure 2.A.10). Given differences in respective forest ages, and a necessity for timber extraction due to high wind-throw risks and contractual obligations, the management of the two forests as a linked system offers increased flexibility for harvesting to help maintain sufficient mature, seed-bearing habitat for a viable red squirrel population.

The results from the model study have been incorporated into the proposed forest design plans for the Kidland and Uswayford region (under the Forestry Commission Cheviot Forest Plan proposal; pers. comm.). The revised plan is currently going through an approval procedure by the Forestry Commission and recommends a combination of forest design scenarios C and D for the harvesting and replanting strategy for these forests. Moreover, model findings highlighted the importance of a dispersal corridor between the two forests. Increasing the habitat linkage between the forests could in the long term help connectivity and provide a permanent corridor between the forests (but this is out with the scope of the Forestry Commissions proposals). In general, the processes followed in this study have been an exemplar for how academic research can have a direct input to land management on the ground that helps managers objectively balance the differing pressures of multi-purpose forestry.

2.A Supplementary information: Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel

The material in this appendix is ordered in the manner in which it is cited in the main document.

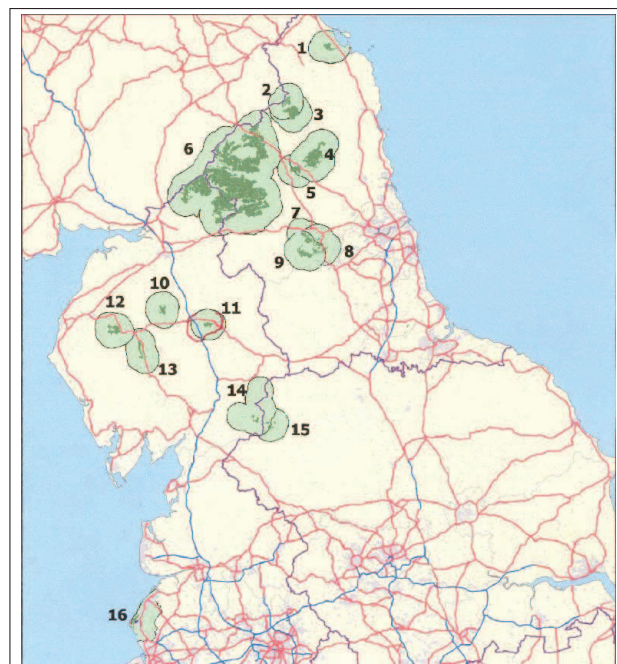


Figure 2.A.1: Map of the Forestry Commission red squirrel reserve areas in northern England. Uswayford is labelled as 2 and Kidland is labelled as 3 (Lurz et al., 2007).

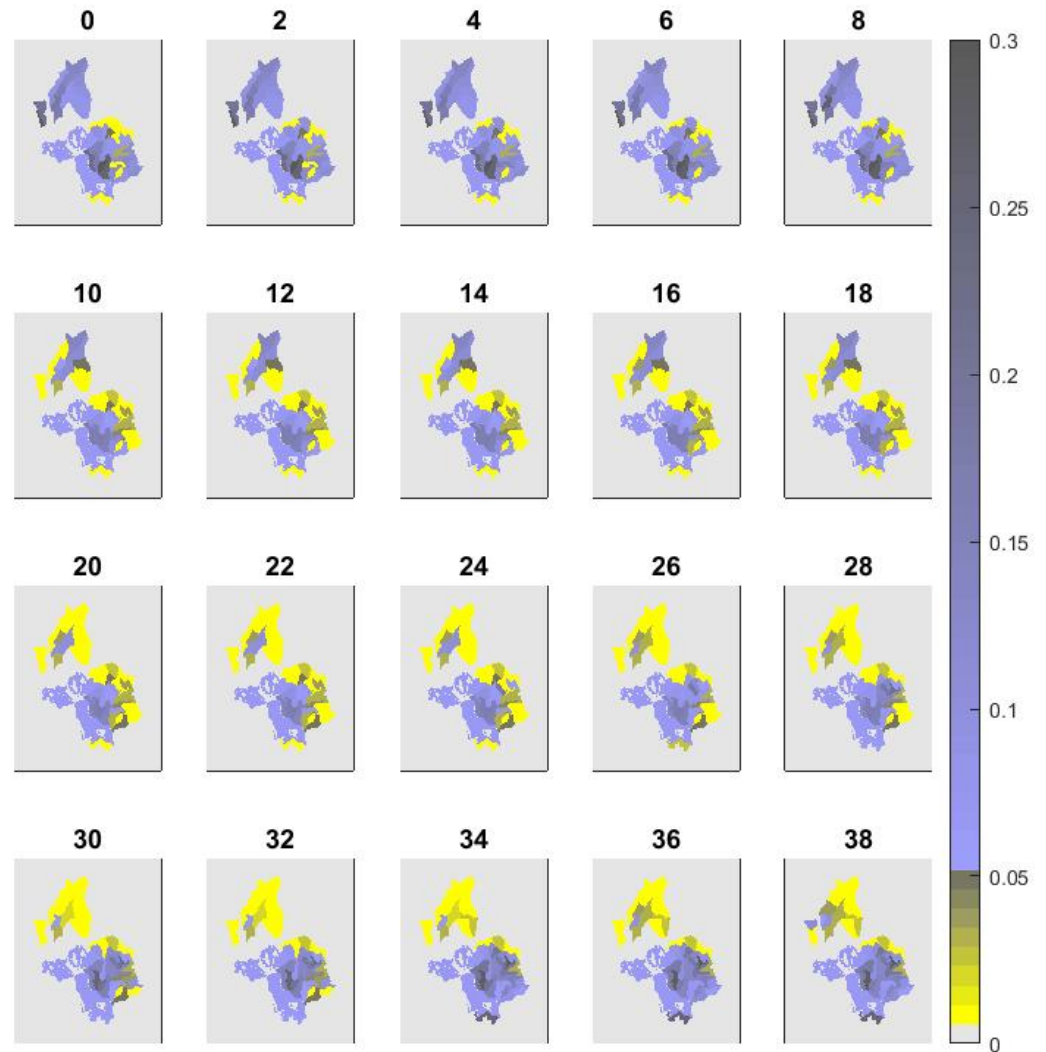


Figure 2.A.2: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the high estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario A.

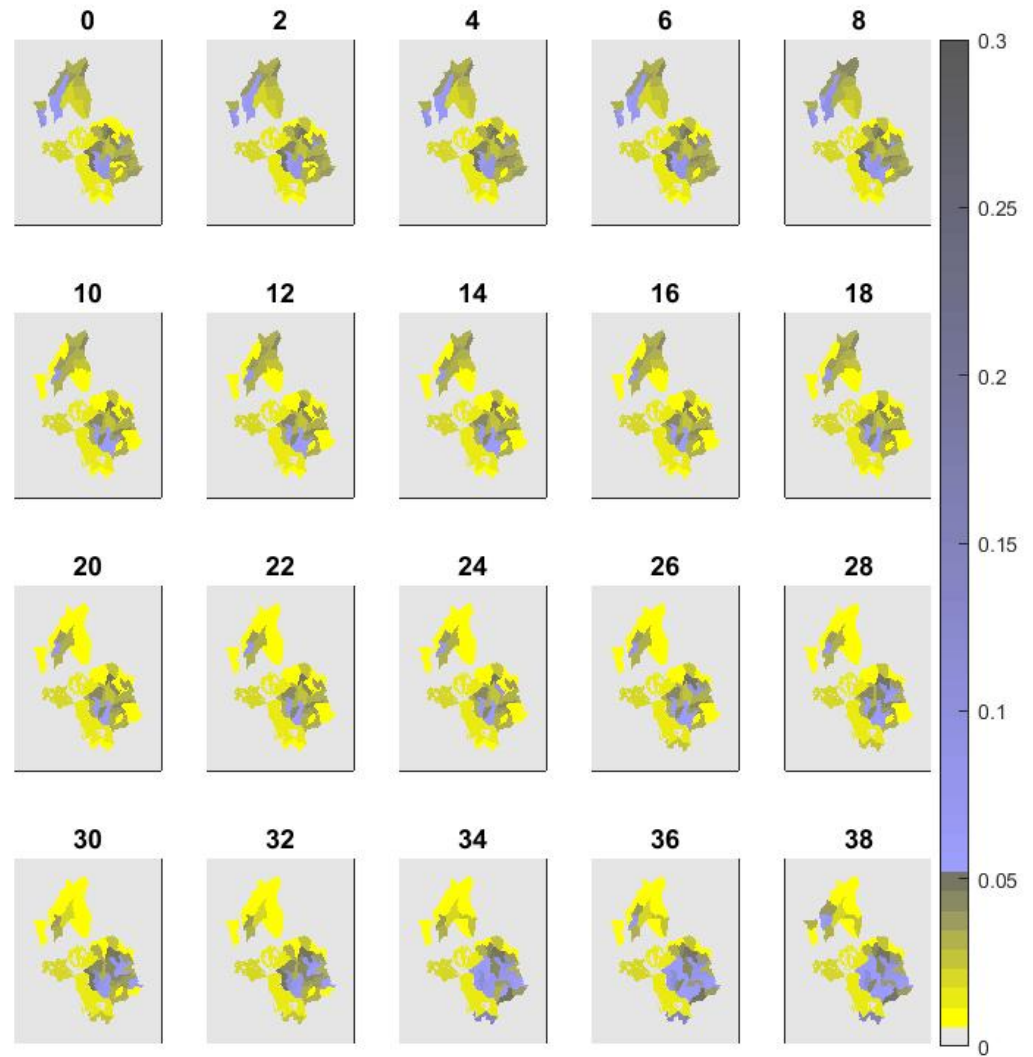


Figure 2.A.3: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the low estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario A.

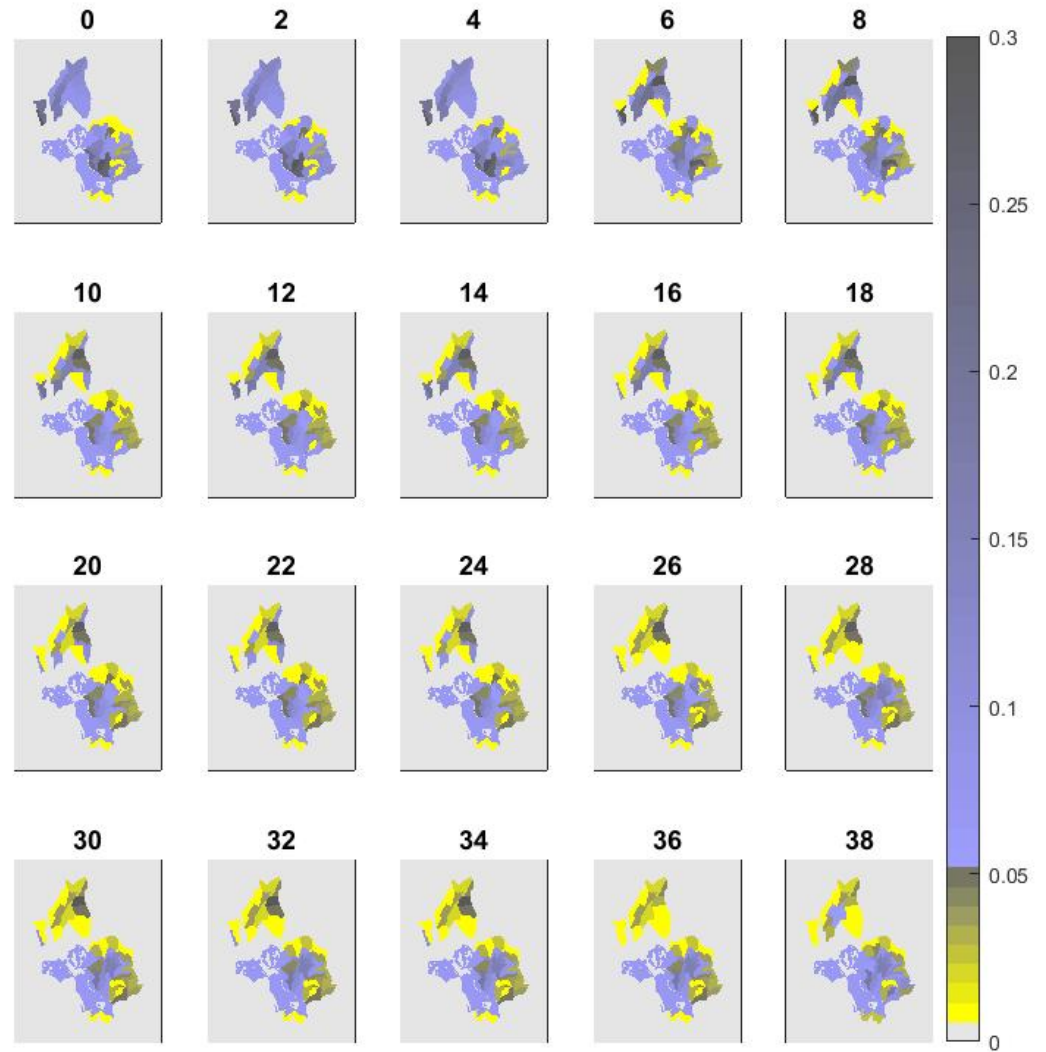


Figure 2.A.4: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the high estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario B.

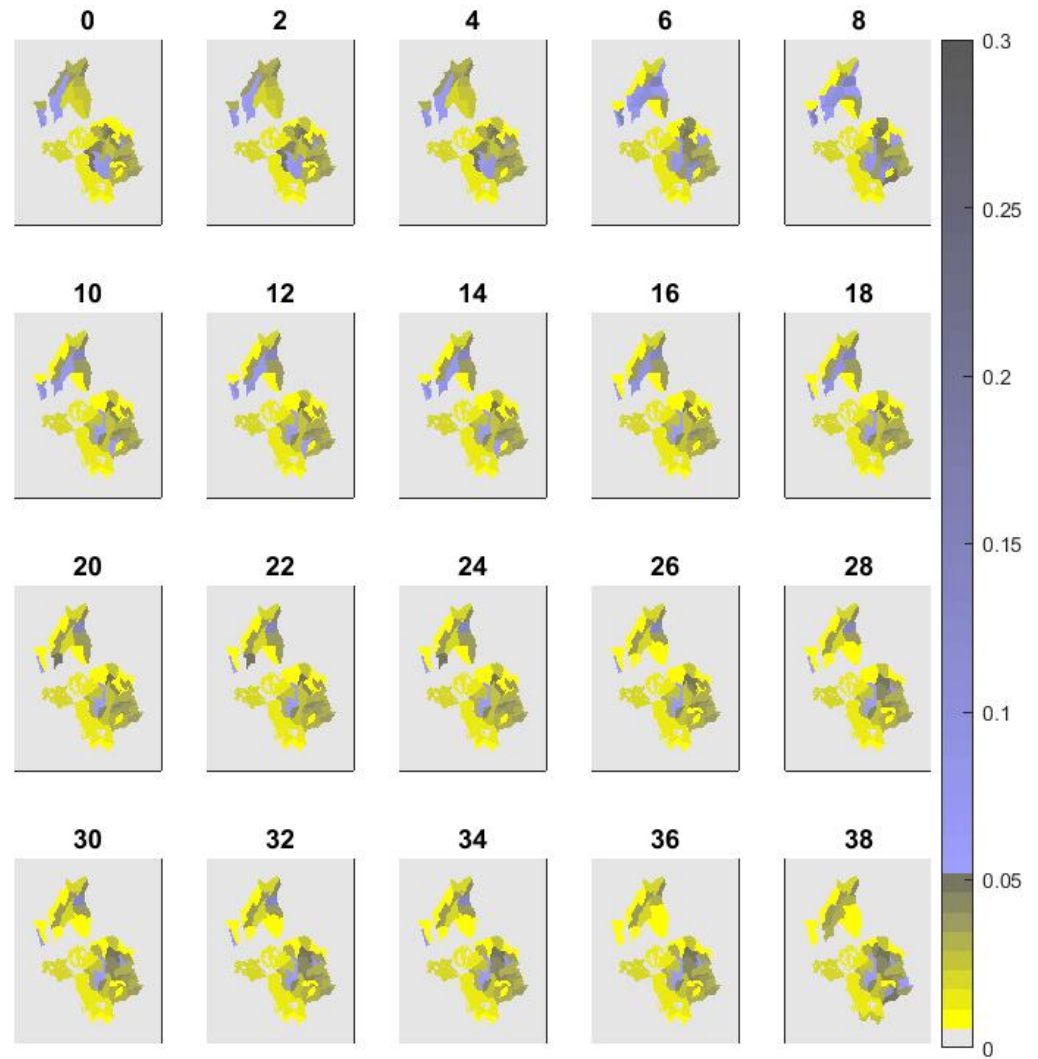


Figure 2.A.5: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the low estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario B.

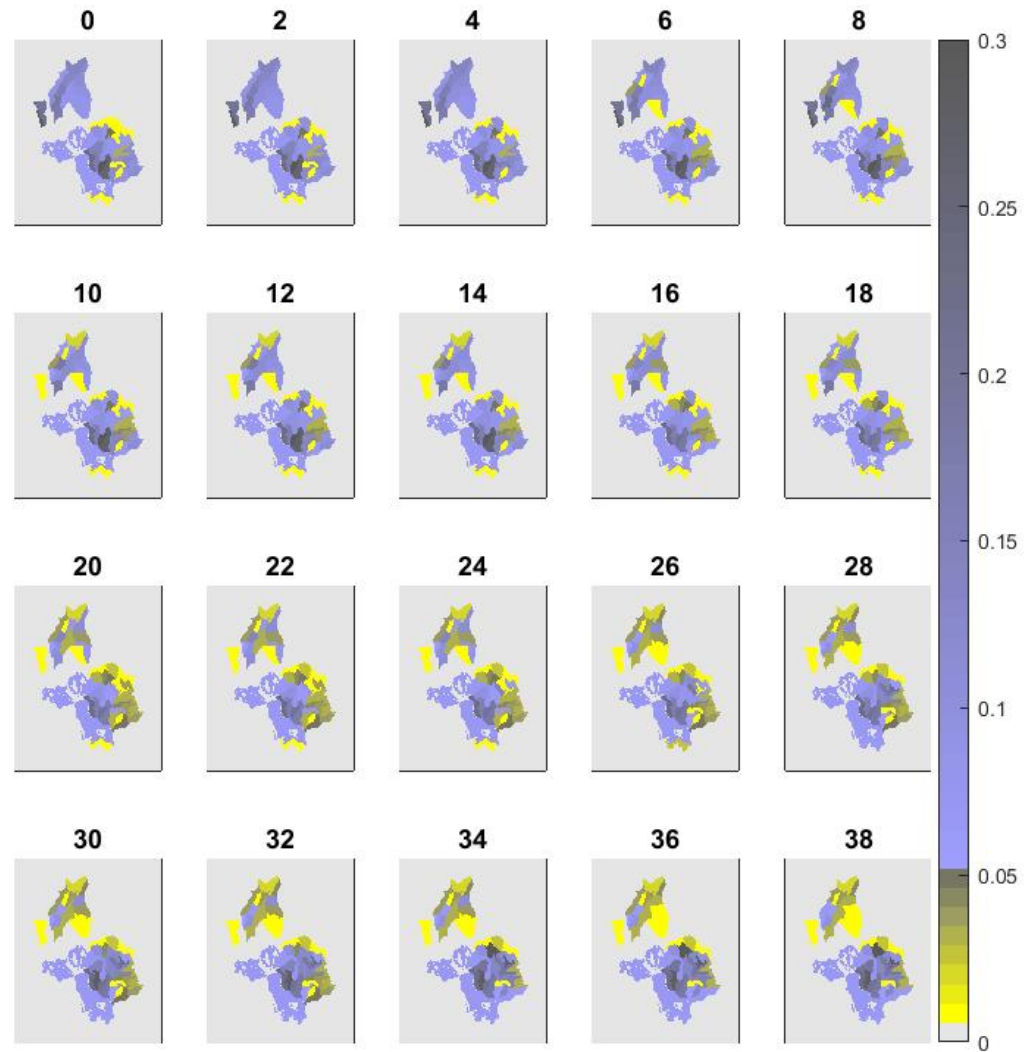


Figure 2.A.6: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the high estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario C.

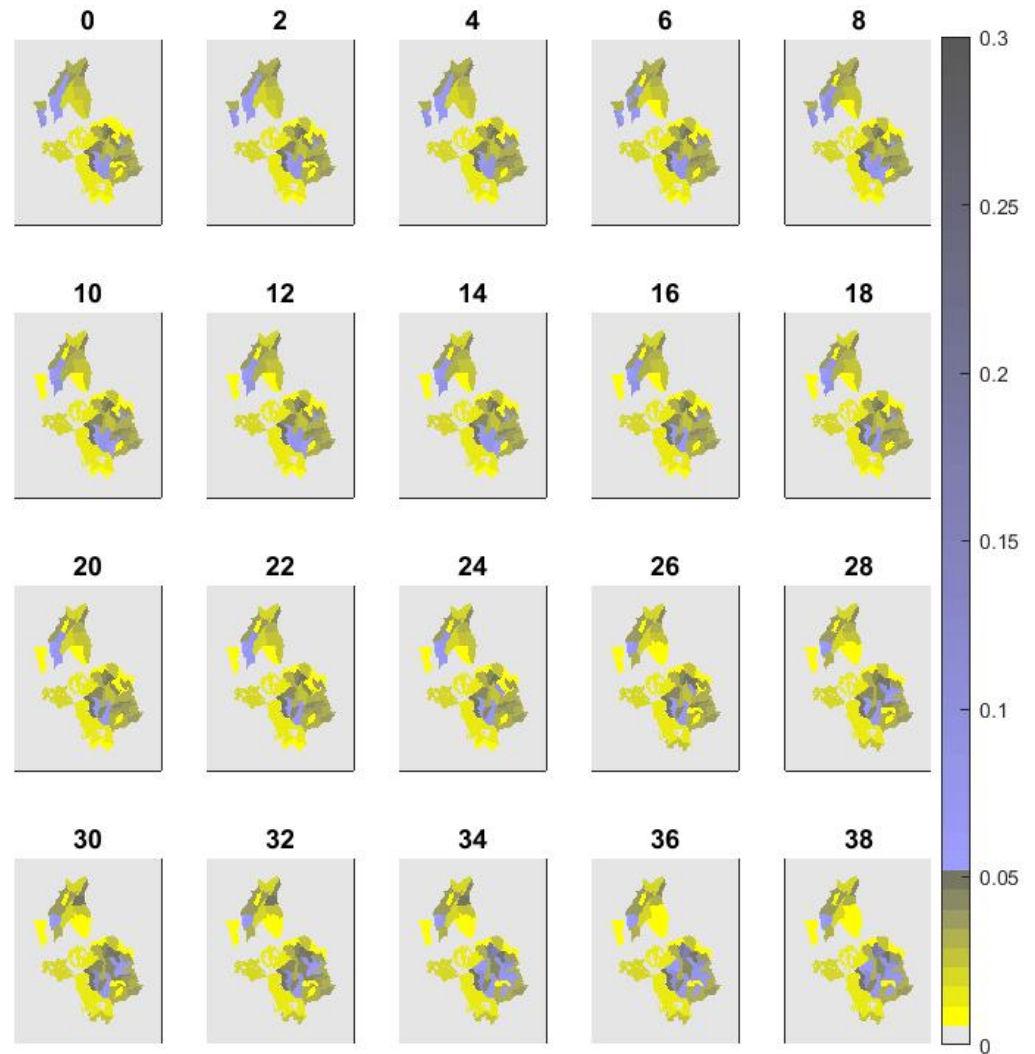


Figure 2.A.7: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the low estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario C.

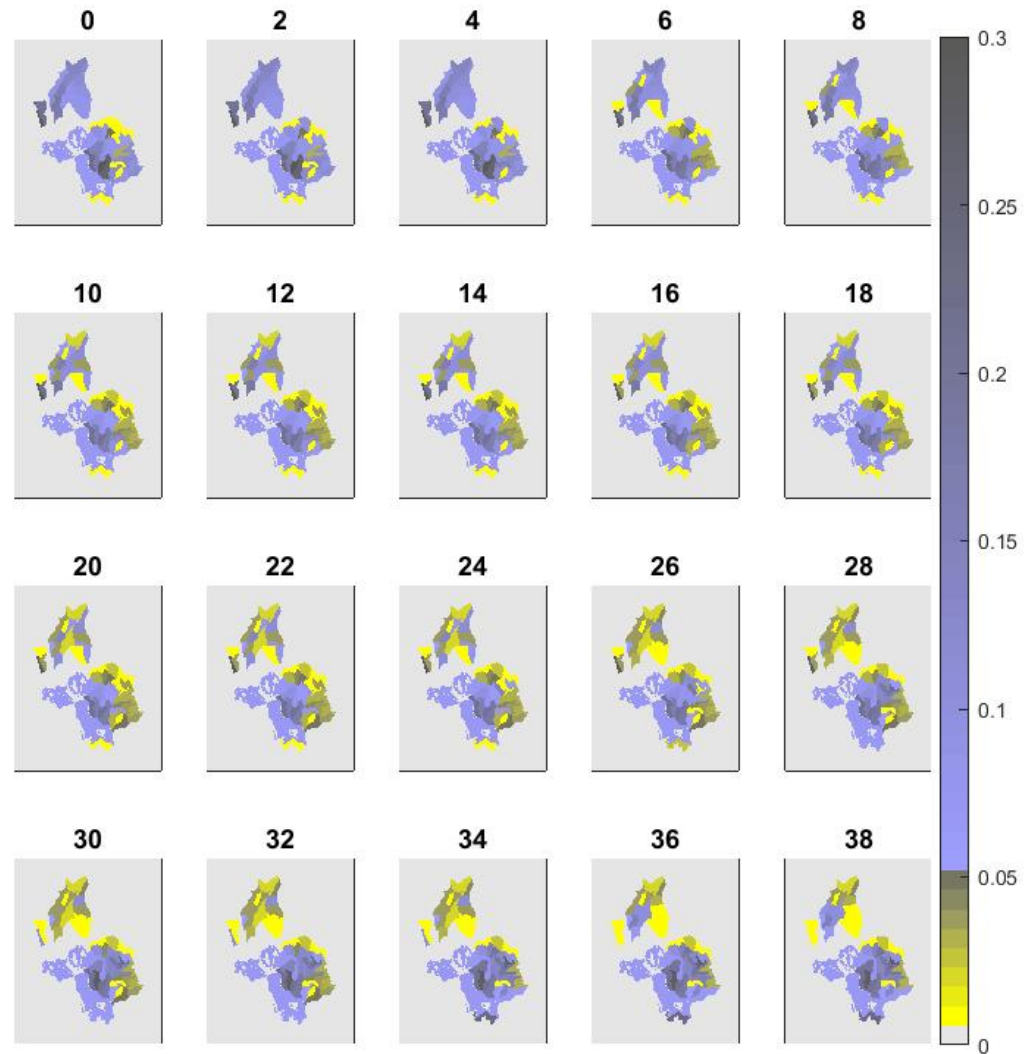


Figure 2.A.8: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the high estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario D.

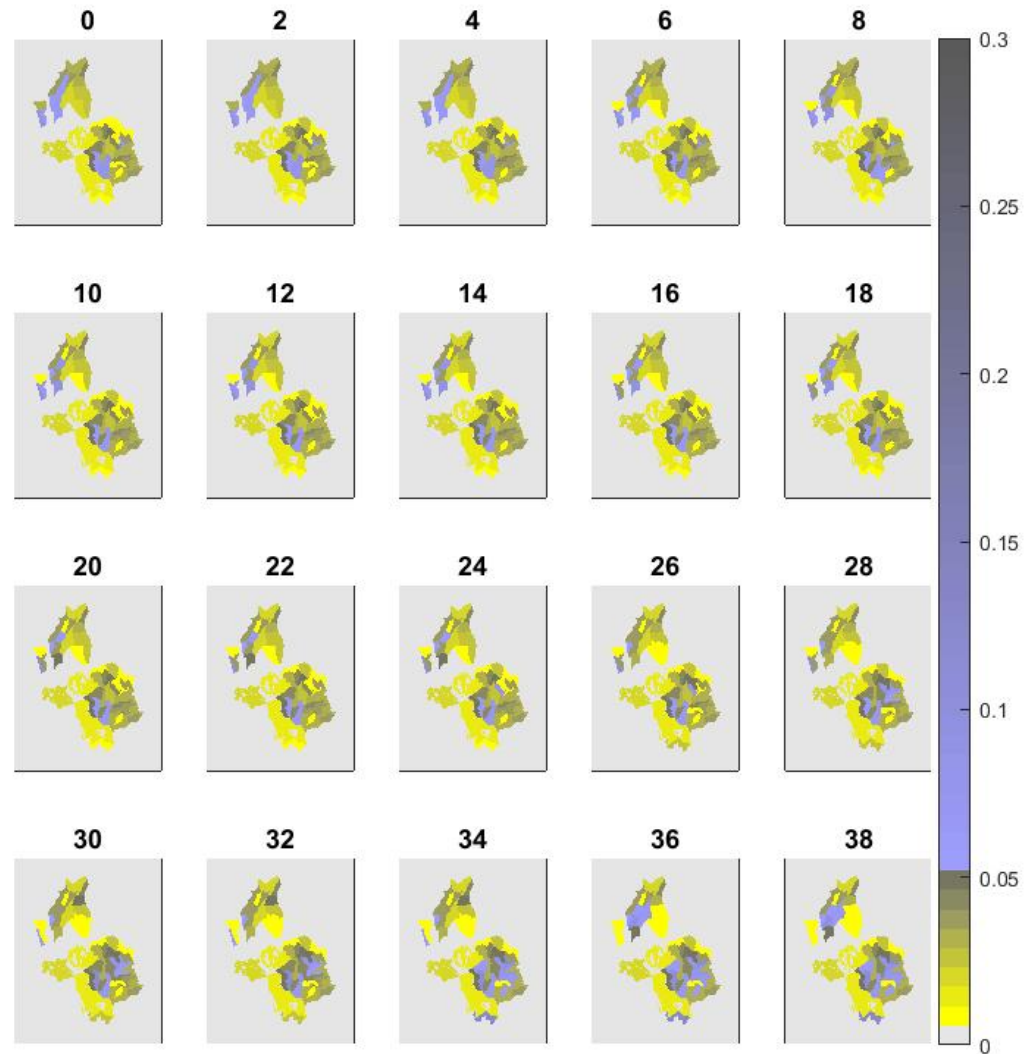


Figure 2.A.9: Snapshots of the red squirrel carrying capacity (squirrels/ha) using the low estimates for Kidland, Uswayford and Tilhill for 2012 (Year 0) to 2050 (Year 38) for scenario D.

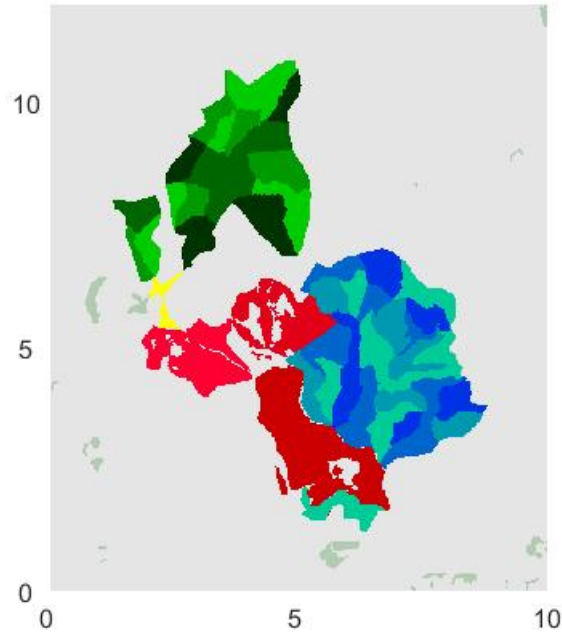


Figure 2.A.10: A map showing the location of a proposed dispersal corridor (yellow) between Kildand/Tilhill (red) and Uswayford (green).

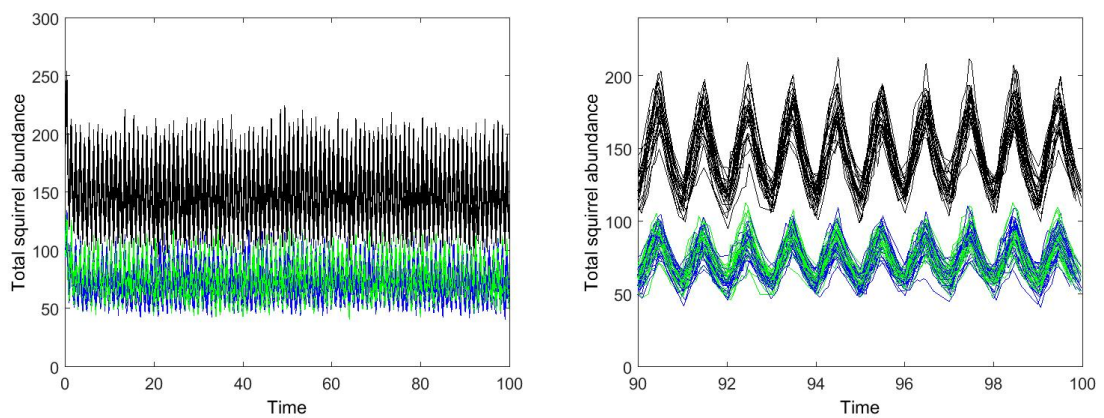


Figure 2.A.11: Realisations showing the 100 year spin-up for the scenario A forest design plans and the high density estimates for 2012 (see Figure 2.2 and Table 2.1) with the combined population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black). The left figure shows the full 100 year spin-up and the right figure the final 10 years of the spin-up.

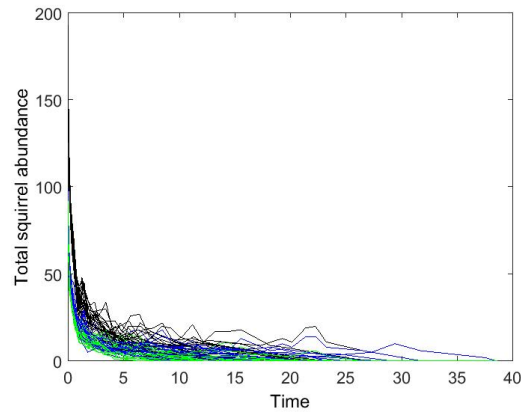


Figure 2.A.12: Realisations showing the spin-up for the scenario A forest design plans and the low density estimates for 2012 (see Figure 2.2 and Table 2.1) with the combined population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black). In all realisations the populations become extinct.

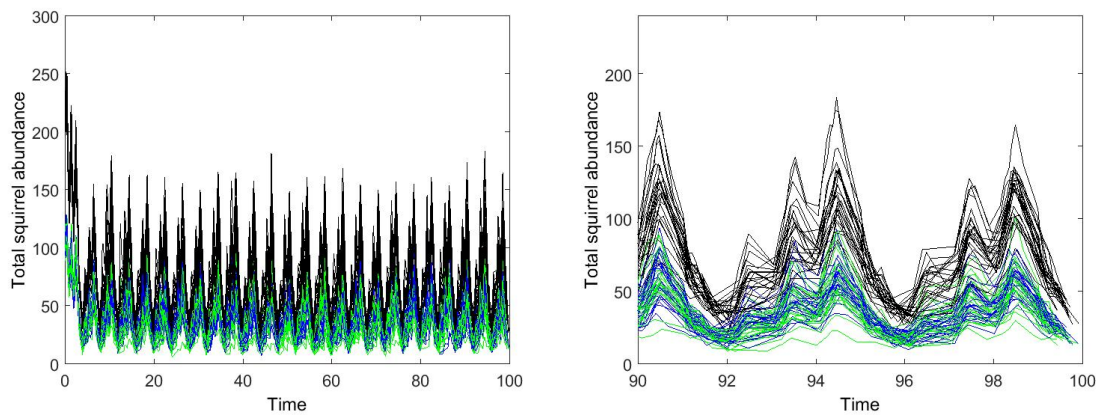


Figure 2.A.13: Realisations showing the 100 year spin-up for the scenario A forest design plans and the 3 high 1 low carrying capacity scenario for 2012 with the combined population abundance in Kidland (blue), Uswayford (green) and both (Kidland + Uswayford; black). The left figure shows the full 100 year spin-up and the right figure the final 10 years of the spin-up.

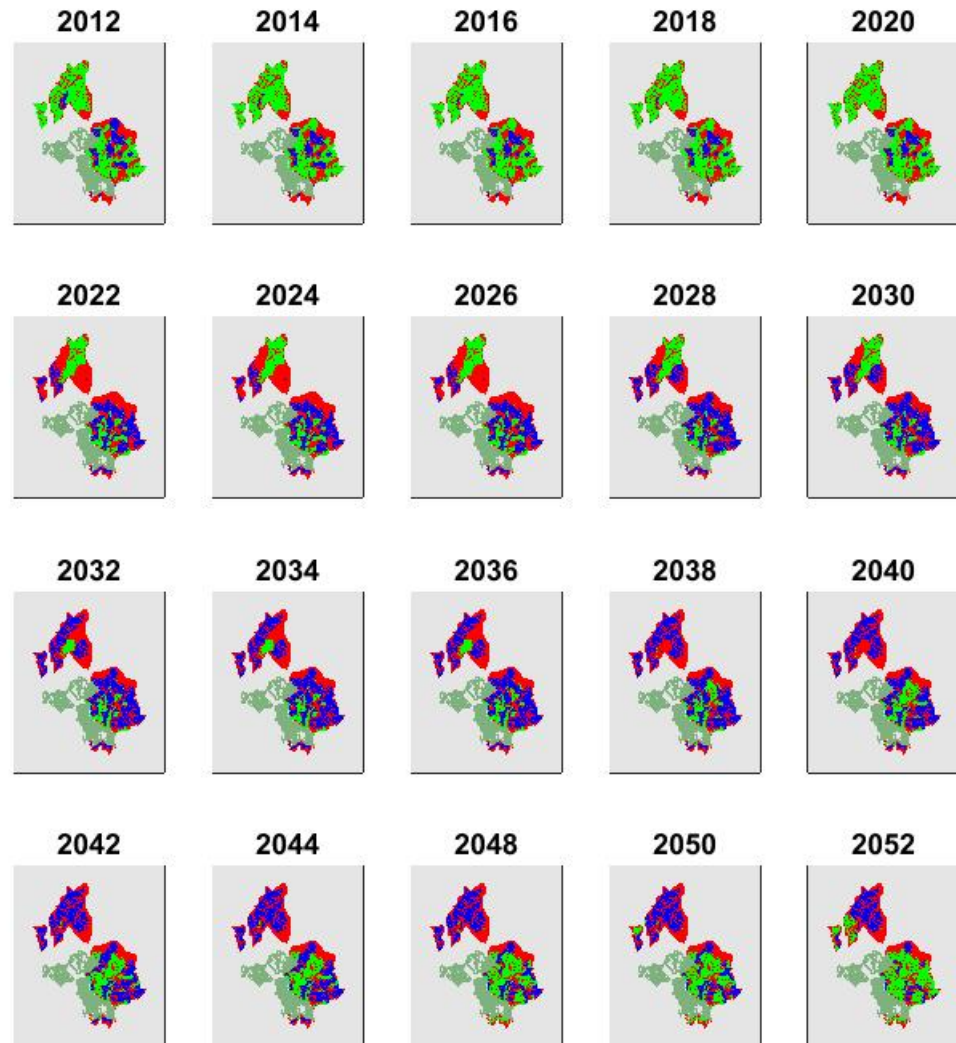


Figure 2.A.14: Maps showing the distribution of mature forest (greater than 30 years old) (green), immature forest (blue), no trees (red) and Tilhill (dark green) based on the forest design plans of scenario A for 2012 - 2052.

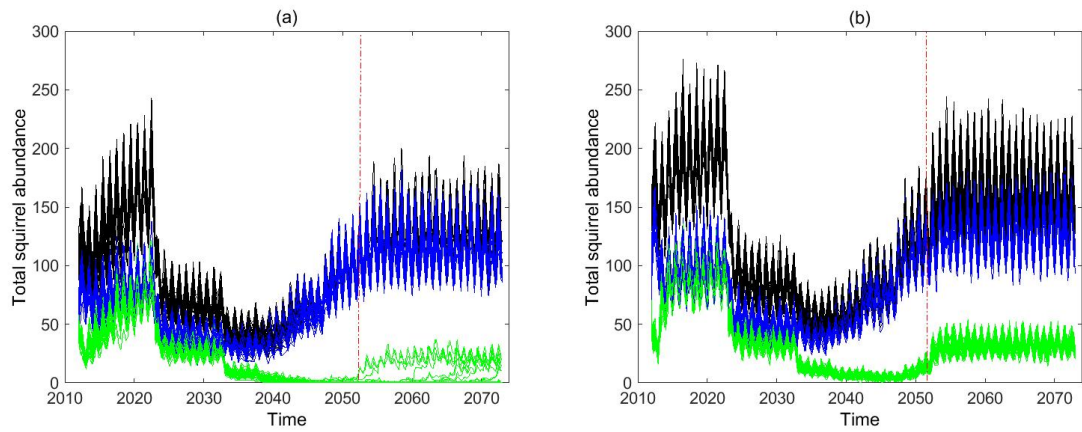


Figure 2.A.15: (a) The population abundance in Kidland (dark grey), Uswayford (light grey) and both (Kidland + Uswayford; black) in the high carrying capacity scenario using the scenario A forest design plan for 2012-2052. The model was continued for an additional 20 years at the 2052 levels (highlighted by the dashed red line). (b) The same scenario as (a) with global dispersal (rather than the restriction of 1km to dispersal).

Chapter 3

Mathematical models of grey squirrel invasion: a case study on Anglesey

This chapter is based on the peer reviewed book chapter:

Jones, H. E., White, A., Lurz, P. W. W., Boots, M., Shuttleworth, C., (2016) Mathematical models of grey squirrel invasion: a case study on Anglesey. In Shuttleworth, C., Lurz, P., Gurnell, J. (Eds), *The Grey Squirrel: Ecology & Management of an Invasive Species in Europe*. European Squirrel Initiative.

The chapter is presented as the published version of the book chapter. The modelling work and writing of the chapter were mainly completed by me. In addition we have enhanced it by citing supporting information that is presented in an appendix at the end of the chapter.

3.1 Summary

A spatial, stochastic model to represent the dynamics of red and grey squirrels and squirrelpox infection is developed to understand the documented replacement of red squirrels by greys which occurred on the Isle of Anglesey between approximately 1966-1998. The model results compare well with the observed historical field data and indicate that competition was the key process responsible for red squirrel decline. Squirrelpox infection, which was prevalent in grey squirrels both on the mainland and latterly as they colonised Anglesey, failed to spread extensively through the resident red squirrel populations on the island. Model findings showed that disease outbreaks may occur in relatively high density red squirrel populations at the local level where reds were sympatric to greys, but at the larger scale red squirrel densities were too low and/or too fragmented to maintain continual intra-specific spread

of pathological infection. This finding has important consequences for applied conservation management and suggests that pathological squirrelpox outbreaks may be localised and the risk of extensive squirrelpox spread through low density red squirrel populations may be low.

3.2 Mathematical models of the grey squirrel invasion

The introduction and invasion of exotic organisms has often caused, and continues to cause, catastrophic damage to native species and ecological communities (Kolar and Lodge, 2001; Ehrenfeld, 2011; Simberloff, 2011; Martin-Albarracin et al., 2015). Understanding the mechanisms and processes that determine successful invasion are therefore key challenges for ecological theory (Manchester and Bullock, 2000; Sutherland et al., 2006). Mathematical models are important tools that can be used to understand ecological invasions. These model frameworks can underpin applied conservation efforts to protect native species and be used to develop management strategies that aim for effective temporal and spatial targeting of resources and actions.

A well-known and important example of ecological invasion is the replacement of the native red squirrel (*Sciurus vulgaris*) by the introduced North American grey squirrel (*Sciurus carolinensis*) in the United Kingdom. Since its introduction, the grey squirrel has replaced the native red squirrel throughout most of England and Wales, and in parts of Scotland and Ireland (Bryce, 1997; O'Teangana et al., 2000; Gurnell et al., 2004; Halliwell et al., 2015). Grey squirrels are now abundant throughout the UK with the exception of the Highlands of Scotland. Red squirrel populations remain widespread in northern Scotland but are often fragmented elsewhere in northern Britain. In southern and central Scotland and across northern England, red squirrel populations are typically sympatric with grey squirrels. Two small mainland populations persist on Wales, and both are largely sympatric with grey squirrels (Halliwell et al., 2015). Conserving the remaining red squirrel populations either by preventing further range expansion of grey squirrel populations, or by removing sympatric grey squirrels are major red squirrel conservation priorities (DEFRA, 2007; Parrott et al., 2009; Forum, 2009; Forestry Commission Scotland, 2012; Schuchert et al., 2014).

Mathematical modelling has been influential in understanding the drivers of invasion in the UK squirrel system. The first mathematical models considered the potential competitive differences between the two species (Okubo et al., 1989; Rushton et al., 1997). These studies indicated that competition could cause the replacement

of red squirrels by grey squirrels, but these early models could not fit the observed expansion of grey squirrels. The model systems were modified to include the role of squirrelpox virus (SQPV; (Rushton et al., 2000; Tompkins et al., 2003)) an asymptomatic infection carried by, but harmless to, grey squirrels, yet producing pathological disease when spread to red squirrels (McInnes et al. (2006); Sainsbury et al. (2008)). These mathematical studies indicated that the disease was critical in the invasion process, could increase the rate of replacement of red squirrels (Tompkins et al., 2003; Rushton et al., 2006) and models that included both competitive and disease processes showed a good fit to observed data (Tompkins et al., 2003). Mathematical models therefore played a key role in shaping the current view that squirrelpox is unequivocally linked to the replacement of red squirrels (Bosch and Lurz, 2012; Lurz, 2015). An acceptance of the central role of squirrelpox has had an impact on both policy and practice to protect red squirrels. Consequently, a priority is given to the control of grey squirrel numbers in order to prevent the spread of squirrelpox and to protect red squirrels in priority conservation areas (such as landscape forest areas defined as ‘strongholds’) (Parrott et al., 2009; Forestry Commission Scotland, 2012; Gurnell et al., 2015).

Mathematical models have been developed to assess the level of grey control required to protect red populations and to prevent the spread of squirrelpox (White et al., 2014, 2016a). They have indicated that while control can prevent grey squirrels from establishing within strongholds, it cannot prevent inter-specific spread of squirrelpox to red squirrels within such priority conservation areas, resulting in periodic outbreaks of disease and mortality in red populations. These disease outbreaks lead to a local crash in red squirrel population abundance, potentially taking several years for red populations to return to pre-infection levels (Chantrey et al., 2014; White et al., 2014, 2016a; Lurz, 2015). Typically, these studies have assessed the role of disease in medium to high density squirrel populations (0.5 - 2 squirrels per hectare). Models have also examined the potential spread of squirrelpox in red (only) populations at low density (0.05 - 0.2 per hectare, see Macpherson et al. (2016a)) and indicate that the impact of associated pathological disease may be significantly reduced as infectious outbreaks may be localised, with squirrelpox failing to spread extensively.

Many of the remaining red squirrel populations in Wales, northern England and southern Scotland are associated with coniferous forests dominated landscapes and broadleaved habitats that support relatively low density squirrel populations. It is therefore important to understand the potential replacement of red squirrels by grey squirrels and the role of squirrelpox in such settings. To examine this, we will focus on the case study system of the invasion of grey squirrels and replacement of red squirrels on Anglesey, Wales, in which the habitat is fragmented with

patches of better quality habitat in the south and east of the island, but where generally population densities are relatively low. We will develop a stochastic, spatial, mathematical model of the red-grey-squirrelepox system that includes a realistic representation of the habitat on Anglesey. Our objectives will be to determine whether squirrelepox is a critical driver in red squirrel replacement in habitats that support low density populations and examine the persistence and variation in squirrelepox prevalence within grey squirrel populations. This information is important for conservation management as these squirrel density characteristics represent many of the regions in which red squirrels still persist in the Britain and Ireland and where conservation management measures are implemented to protect them.

3.3 The replacement of red squirrels on Anglesey

The 710km² Isle of Anglesey is located off the coast of north-west Wales. The island is separated from the mainland by the Menai Strait, with the Menai Bridge (1826) and the dual level Britannia Bridge (1850/1972) connecting the island to the mainland. The lower rail deck level of the Britannia Bridge is thought to provide a suitable corridor for squirrels to enter or leave the island (Shuttleworth, 2016), with suitable habitat for squirrels extending to the waterfront at either end of the bridge (Figure 3.1). Until the 1960s, Anglesey was inhabited only by red squirrels (Walker, 1968). However, grey squirrels were recorded moving west along the north Wales coast, reaching Flintshire and Denbighshire (1945-1952), before being recorded in Caernarvonshire (Gwynedd) in the late 1950s (Shorten, 1954). In 1966, the first grey squirrels were reported on Anglesey (Walker, 1968) although it is possible that incursions had taken place a few years earlier. Between (approximately) 1966 and 1998, grey squirrels established and continued to spread on Anglesey before almost completely replacing red squirrels. In the late 1990s, only 40 animals remained within a spruce dominated stand (Shuttleworth, 2003). Therefore, Anglesey provides a relatively unique case study for modelling the squirrel systems, with clear initial conditions (c. 1966) of red squirrels at their carrying capacity with the first grey squirrel incursions present, and clear end conditions (in 1998) of red squirrels almost completely replaced across the island by grey squirrels. Moreover, grey squirrels on the mainland and island have been shown to be sero-positive for squirrelepox (Shuttleworth et al., 2015a) and so this case study system also offers further opportunity to examine the impact of squirrelepox on invasion and replacement of red squirrels.



Figure 3.1: A map of Anglesey (left; ©OpenStreetMap contributors), a photograph of the lower level of the Britannia Bridge which provides a dispersal corridor between the mainland and Anglesey (middle; ©Hannah Jones) and a photograph of the habitat surrounding the bridge which enables squirrels to gain access to the bridge (right; with squirrel ecologists and modellers enjoying the sunshine ©Peter Lurz).

3.4 A mathematical model of the Anglesey squirrel system

3.4.1 Calculating Potential Density

Using GRASS GIS version 6.4 (GRASS Development Team, 2016), we converted digital land cover vector maps for Anglesey and the adjacent mainland (supplied by Natural Resources Wales) into a 25 m by 25 m raster map with each entry representing the dominant habitat type. The raster map data was combined with estimates of red and grey squirrel density in different habitat types (Table 3.1) for each 25 m by 25 m class and summed to provide the potential density of red and grey squirrels at a 1 km by 1 km patch level (this scale has been used successfully

to model the UK squirrel system in previous studies (White et al., 2014, 2016a; Macpherson et al., 2016a)).

Table 3.1: Squirrel densities per ha for different habitat types present on Anglesey and the surrounding mainland. (Data taken from Bosch and Lurz (2012); Gurnell (1983, 1996a); Shuttleworth et al. (2012)).

Habitat	Red squirrels (/ha)			Grey squirrels (/ha)		
	Low	Medium	High	Low	Medium	High
semi-natural broadleaved woodland	0.30	0.65	1.00	1.00	2.50	4.00
planted broadleaved woodland	0.30	0.65	1.00	1.00	2.50	4.00
semi-natural coniferous woodland	0.20	0.35	0.50	0.20	0.6	1.00
planted coniferous woodland	0.20	0.35	0.50	0.20	0.6	1.00
semi-natural mixed woodland	0.30	0.65	1.00	0.50	1.25	2.00
planted mixed woodland	0.30	0.65	1.00	0.50	1.25	2.00
dense scrub	0.10	0.25	0.40	0.30	0.65	1.00
introduced scrub	0.10	0.25	0.40	0.30	0.65	1.00
gardens	0.15	0.315	0.48	0.38	0.94	1.50
caravan site	0.08	0.16	0.24	0.19	0.47	0.75

3.4.2 The model framework

The population dynamics of red and grey squirrels and squirrelpox infection are represented by the spatial, stochastic model outlined in White et al. (2014) and White and Lurz (2014). A stochastic model is required because it can represent the chance of extinction or disease fade-out at low density. This framework has been used successfully to examine the impact of squirrelpox on grey squirrel invasion in red squirrel strongholds (White et al., 2014) and on realistic landscapes (White and Lurz, 2014). The model is modified further to include seasonality, assuming births occur for six months of the year (between March and September), while other life-history and disease processes operate throughout the year. The inclusion of seasonality means that the population density oscillates with an annual signal around the potential density and in particular, can be above the potential density towards the end of the breeding season. This surplus triggers an increase in squirrel dispersal and better reflects the dynamics of the natural system (Macpherson, 2014). The stochastic population model is developed by modifying an underlying deterministic system of Tompkins et al. (2003) which represents the dynamics of susceptible and infected reds (S_R , I_R) and susceptible, infected and immune greys (S_G , I_G , R_G). The deterministic model is as shown in Equations 3.2-3.5. Further details of the underlying deterministic model and in particular an assessment of the impact of the seasonal birth on the epidemiological dynamics are given in the Appendix 3.A.

$$\frac{dS_G}{dt} = A_G(t) - bS_G - \beta S_G(I_G + I_R) \quad (3.1)$$

$$\frac{dI_G}{dt} = \beta S_G(I_G + I_R) - bI_G - \gamma I_G \quad (3.2)$$

$$\frac{dR_G}{dt} = \gamma I_G - bR_G \quad (3.3)$$

$$\frac{dS_R}{dt} = A_R(t) - bS_R - \beta S_R(I_G + I_R) \quad (3.4)$$

$$\frac{dI_R}{dt} = \beta S_R(I_G + I_R) - bI_R - \alpha I_R \quad (3.5)$$

where $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total squirrel populations and

$$\text{where } A_G(t) = \begin{cases} a_G (1 - q_G(H_G + c_R H_R)) H_G & t_n \leq t < t_{n+1} + 0.5 \\ 0 & t_n + 0.5 \leq t < t_{n+1} \end{cases}$$

represents the periodic birth rate of grey squirrels which assumes births occur for only half of the year (between March and September each year). The term for $A_R(t)$ (Eqn. 3.4) is equivalent to $A_G(t)$ (Eqn. 3.2) with the subscripts for R and G interchanged. In Tompkins et al. (2003) the two species have the same rate of adult mortality ($b = 0.9$: (Barkalow et al., 1970)) but different rates of maximum reproduction ($a_R = 3$, $a_G = 3.4$ adapted from Tompkins et al. (2003) to account for seasonality). The competitive effect of grey squirrels on red squirrels is denoted by $c_G = 1.65$, whilst that of red squirrels on grey squirrels is denoted by $c_R = 0.61$ (Bryce, 1997). Squirrelpox virus is transmitted (both within and between each squirrel species) with coefficient $\beta = 3.27$ (following the method of Tompkins et al. (2003) to match the sero-prevalence on the mainland adjacent to Anglesey of 67%, (Schuchert et al., 2014)). Infected red squirrels die due to the disease at rate $\alpha = 26$ and infected greys recover at rate $\gamma = 13$ (Tompkins et al., 2003). The susceptibilities to crowding (q_R , q_G) are set to ensure the average density over one year is equal to the potential density in each 1 km by 1 km grid cell. To generate the stochastic model, the rates in the deterministic model are converted to probabilities of events that account for changes in individual patch level abundance (Renshaw, 1991). The probabilities are shown in Table 3.2.

Table 3.2: The stochastic model within each one km grid cell indicating the probability of different events. $R = \sum[\text{rates}]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (and are set to zero otherwise). Due to daily squirrel movement within a core range of radius, $\theta = 0.15\text{km}$, squirrelpox transmission can occur from infected squirrels within the focal grid cell and also from the eight neighbouring grid cells (with adjacent and corner cells weighted appropriately). The dispersal term is shown for class S_G only, but is similar for all other classes. The model assumes density dependent dispersal, such that squirrel dispersal increases as density increases and the dispersal rate is $m = 2b$, when the patch density is equal to the potential density. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of two km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). Further details of determining the dispersal parameters are shown in Appendix 3.B.

Birth of Grey to S_G	$P(S_G \rightarrow S_G + 1)$	$:[(a_G - q_G (H_G + c_R H_R)) H_G]/R$
Natural Death of S_G	$P(S_G \rightarrow S_G - 1)$	$:[bS_G]/R$
Infection of Grey	$P(S_G \rightarrow S_G - 1, I_G \rightarrow I_G + 1)$	$:[\beta S_G (I_G + I_R)]/R +$ $+ \theta \sum_{\text{Adjacent}} (I_G + I_R) +$ $+ \theta^2 \sum_{\text{Corner}} (I_G + I_R)]/R$
Natural death of I_G	$P(I_G \rightarrow I_G - 1)$	$:[bI_G]/R$
Recovery of Grey	$P(I_G \rightarrow I_G - 1, R_G \rightarrow R_G + 1)$	$:[\gamma_G I_G]/R$
Natural Death of R_G	$P(R_G \rightarrow R_G - 1)$	$:[bR_G]/R$
Birth of Red to S_R	$P(S_R \rightarrow S_R + 1)$	$:[(a_R - q_R (H_R + c_G H_G)) H_R]/R$
Natural Death of S_R	$P(S_R \rightarrow S_R - 1)$	$:[bS_R]/R$
Infection of Red	$P(S_R \rightarrow S_R - 1, I_R \rightarrow I_R + 1)$	$:[\beta S_R ((I_G + I_R) +$ $+ \theta \sum_{\text{Adjacent}} (I_G + I_R) +$ $+ \theta^2 \sum_{\text{Corner}} (I_G + I_R))]/R$
Death of I_R	$P(I_R \rightarrow I_R - 1)$	$:[(b + \alpha) I_R]/R$
Dispersal of S_G	$P(S_G \rightarrow S_G - 1)$	$:[mS_G (H_G + c_R H_R)/K_G]$

The events are incremented at random with the associated probabilities updated due to changes in population density after each event. The time between events is an exponentially distributed random variable and can be determined as $T_{\text{event}} = -\ln(\sigma)/R$ where σ is a random number drawn from a uniform distribution between 0 and 1 (see Renshaw (1991)). The model is coded using Fortran 90 and individual

simulations are undertaken using a Gillespie algorithm and provide information of the behaviour in a single realisation. Multiple realisations are generated to assess the average behaviour and variability (see White et al. (2014) for further details of the model set-up).

To determine which of the estimates of potential density best reflects the densities observed on Anglesey, we ran the model using the low, medium and high density estimates in Table 3.1 (see Figure 3.2). Estimates of the abundance of red and grey squirrels on Anglesey in the absence of the other species are 3000-4000 grey squirrels, (Schuchert et al., 2014), and 700 red squirrels, (Halliwell et al., 2015). These correspond most closely with the medium estimates of density and therefore, we used these values for the remaining analysis. The overestimate in squirrel numbers under medium density values may reflect the fact that the model system does not account for poor seed crops, which would decrease squirrel numbers and in the model system, squirrels can persist on the north-west of Anglesey (Holy Island) but squirrels were not observed here during the 1960s-1990s period. Figure 3.2 also indicated that the suitable squirrel habitat on Anglesey is fragmented. There are patches of better quality habitat in the south and east of Anglesey which are superimposed on a landscape that in general supports relatively low density squirrel populations.

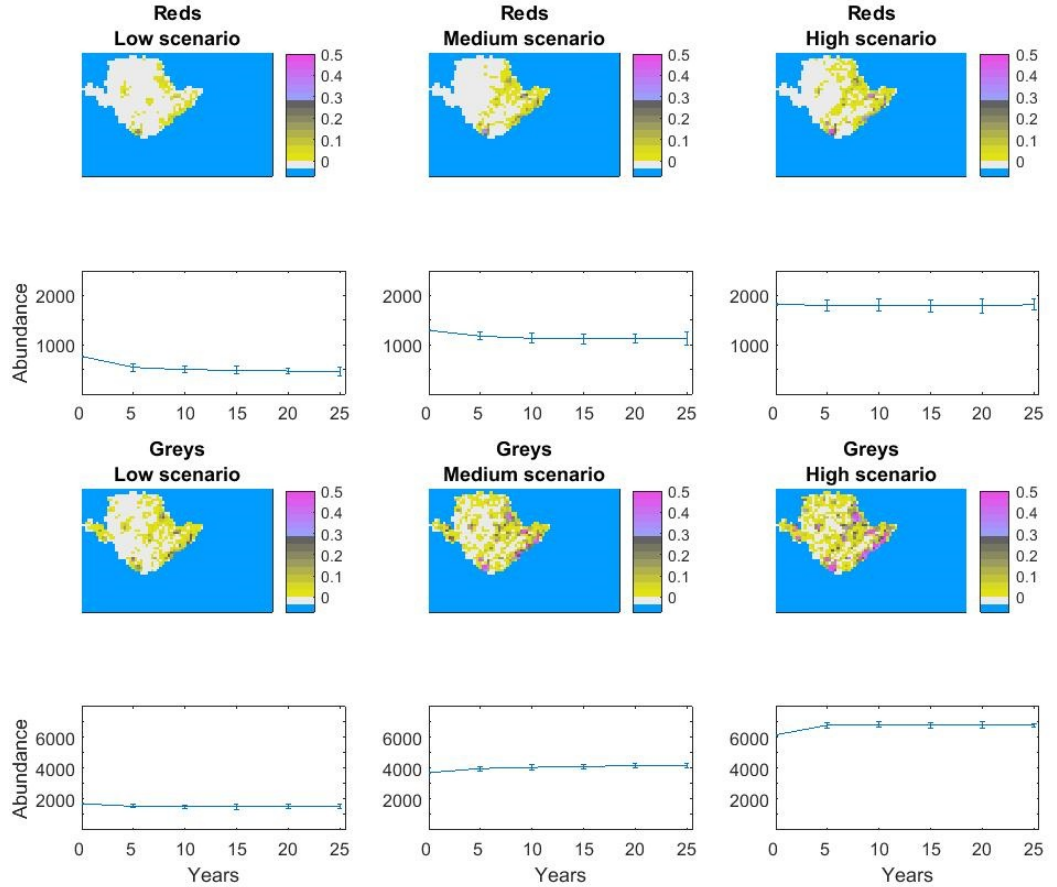


Figure 3.2: A representative model run showing the distribution of red and grey squirrels on Anglesey after 25 years under the different density scenarios detailed in Table 3.1 (the colour bar indicates squirrel density per ha which is determined by dividing the number of squirrels in each one km by one km cell by 100). The line graphs show the corresponding average population abundance on Anglesey over time for 20 model realisations with 95% confidence intervals.

3.5 Model application: the driver of red squirrel replacement on Anglesey

As previously reported, within 35 years, from 1966 to 1998, an almost complete replacement of red squirrels by grey squirrels had occurred on Anglesey. To assess whether the model can reproduce this, we initiated the model with the red squirrel density as in Figure 3.2 (i.e. medium density values but excluding red squirrels from Holy Island in the model to reflect the observed initial distribution) and in-

roduced 25 grey squirrels (of which four were infected with SQPV) into the grid cells adjacent to the Britannia Bridge on Anglesey. The spread of grey squirrels and consequent decline of red squirrels is shown in Figure 3.3. The model captured the observed replacement of red squirrels and the extensive spread of grey squirrels across Anglesey, with an average of only 11 red squirrels left after 35 years.

To examine the impact of squirrelpox on the replacement of red squirrels on Anglesey, we repeated the model simulations but assumed that all 25 grey squirrels introduced on Anglesey were uninfected and that SQPV was absent on the mainland (this simulates the competitive effect only, Figure 3.4). The results for competition-mediated replacement are similar to those when squirrelpox was also included (Figure 3.3). Therefore, the results reported here for Anglesey contradict previous model findings which indicate that squirrelpox increases the rate of replacement of red by grey squirrels significantly (Rushton et al., 2000; Tompkins et al., 2003; White et al., 2014).

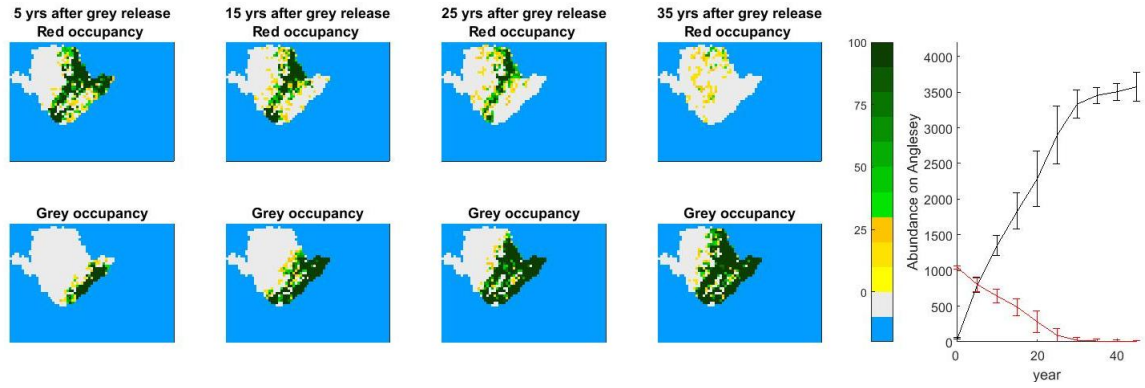


Figure 3.3: The percentage presence of red and grey squirrels over 20 realisations when 25 grey squirrels (of which 4 were infected) were released onto Anglesey at a location adjacent to the Britannia Bridge. Percentage presence is defined as the percentage of realisations in which squirrel density was above zero. The maps show how greys spread across Anglesey and replaced red squirrels. The graph shows how the average abundance of red squirrels (red line) and grey squirrels (black line) changes following the introduction of greys (with 95% error bars). This model set-up was used to undertake a sensitivity analysis of the dispersal parameters. The figures in this study use values of $m=2b=1.8$ and a maximum dispersal distance of 2 km as these values gave the best fit to observed data, see Appendix 3.B for more details.

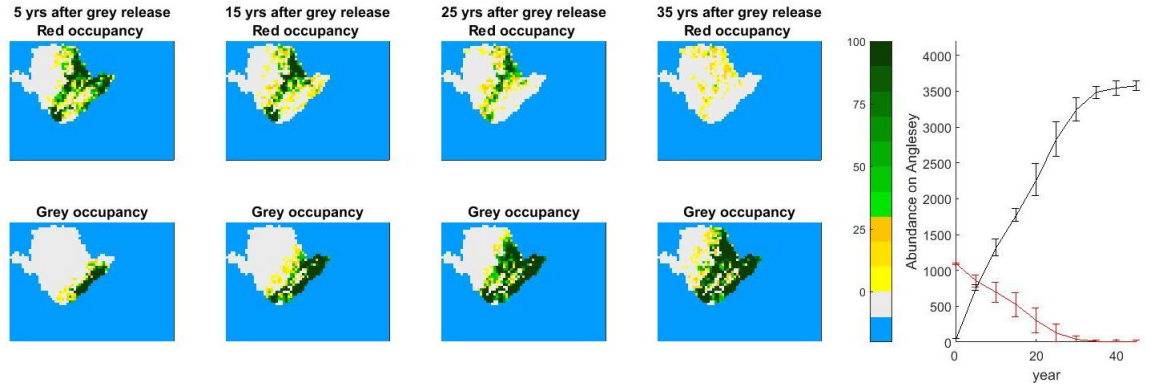


Figure 3.4: The percentage presence of red and grey squirrel over 20 realisations and the change in population abundance when 25 uninfected grey squirrels were released onto Anglesey at a location adjacent to the Britannia Bridge. Percentage presence is defined as the percentage of realisations in which squirrel density was above zero. The graph shows how the average abundance of red squirrels (red line) and grey squirrels (black line) changes following the introduction of greys (with 95% error 307 bars), (other details are as in Figure 3.3).

3.5.1 Squirreldynamics in grey squirrel populations

To understand why squirreldynamics did not increase the rate of replacement of red squirrels on Anglesey in the model, we plotted the prevalence of SQPV in grey squirrels (R_G/H_G) in each grid cell for a typical model realisation (Figure 3.5) and the presence of susceptible and infected red squirrels in each grid cell (Figure 3.6). It is noticeable that the pathological infection (arriving as an asymptomatic infection in grey squirrels) does not spread rapidly through the red squirrel population and only localised disease outbreaks are observed in populations adjacent to grey squirrels (Figure 3.6). The infection also initially fades out within grey squirrel populations on Anglesey and only starts to persist once Anglesey grey squirrel abundance and range has expanded sufficiently to support the infection (after approximately 20 years, Figure 3.5). Even in established grey squirrel populations, SQPV prevalence is observed to fluctuate and fade-out over time (both on Anglesey and the mainland).

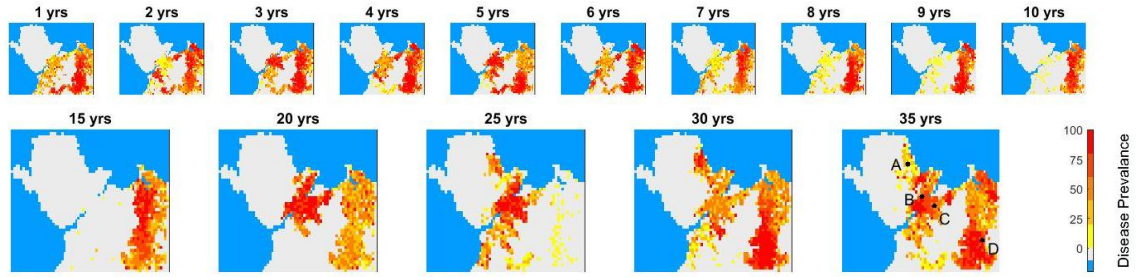


Figure 3.5: Squirrelpox prevalence in grey squirrels for a typical model realisation on Anglesey and the mainland assuming the mainland initially contains grey squirrels with squirrelpox and Anglesey initially contains red squirrels without the disease. 25 grey squirrels (with 4 infected) were introduced to Anglesey adjacent to the Britannia Bridge at time zero. The circles labelled A-D on the final image give the locations at which the epidemiological dynamics are examined in detail in Figure 3.7.

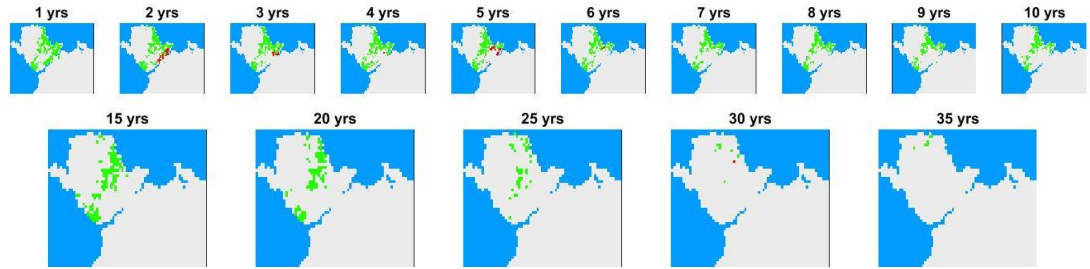


Figure 3.6: Red presence on Anglesey and the mainland for a typical model realisation with the set-up as in Figure 3.5, highlighting where susceptible red squirrels (green shaded cells) and infected red squirrels (red shaded cells) are present over a one year period.

To investigate the epidemiological dynamics in grey squirrels during the replacement, we plotted the abundance of susceptible, infected and recovered/ immune individuals and the infection prevalence for key grid cells (Figure 3.7). These key cells are chosen to highlight how squirrelpox impacts on red squirrel replacement in regions where grey squirrels are initially absent and therefore grey squirrel invasion follows a process of dispersal and expansion (Figure 3.7A) and regions in which squirrelpox is present at the onset of grey squirrel invasion (Figure 3.7B). The key cells are also chosen to examine the epidemiological dynamics, in particular the variation in SQPV prevalence, in established grey squirrel populations on the mainland (Figures 3.7C and 3.7D) and expanding populations on Anglesey (Figures 3.7A and 3.7B). When SQPV is present, there is a clear annual signal in the prevalence. This is driven by seasonality in reproduction and results in peak prevalence

at the end of the breeding season following the infection of (new) susceptible grey squirrels. While SQPV can persist in the long-term, there are periods where the infection may fade-out, before re-establishing due to the spread of infection from neighbouring regions. For instance, SQPV fades out in the region either side of the Britannia Bridge from years 10 to 18 (Figure 3.5, Figures 3.7B and 3.7C) before it is reintroduced through infection spread from populations on the mainland to the east of Bangor. In some regions, red squirrels are replaced by grey squirrels through competitive processes only, before SQPV reaches that cell (Figure 3.7A). However, when squirrelpox is present it can cause high levels of mortality in local red squirrel populations (Figure 3.7B). So while squirrelpox is not expected to spread extensively through red squirrel populations, it can spread locally from grey to red squirrels and have important impacts on red squirrel survival at the local level. This may be of particular significance for the red squirrel populations on Anglesey adjacent to the Britannia Bridge, as this is the most likely dispersal route of grey squirrels from the mainland.

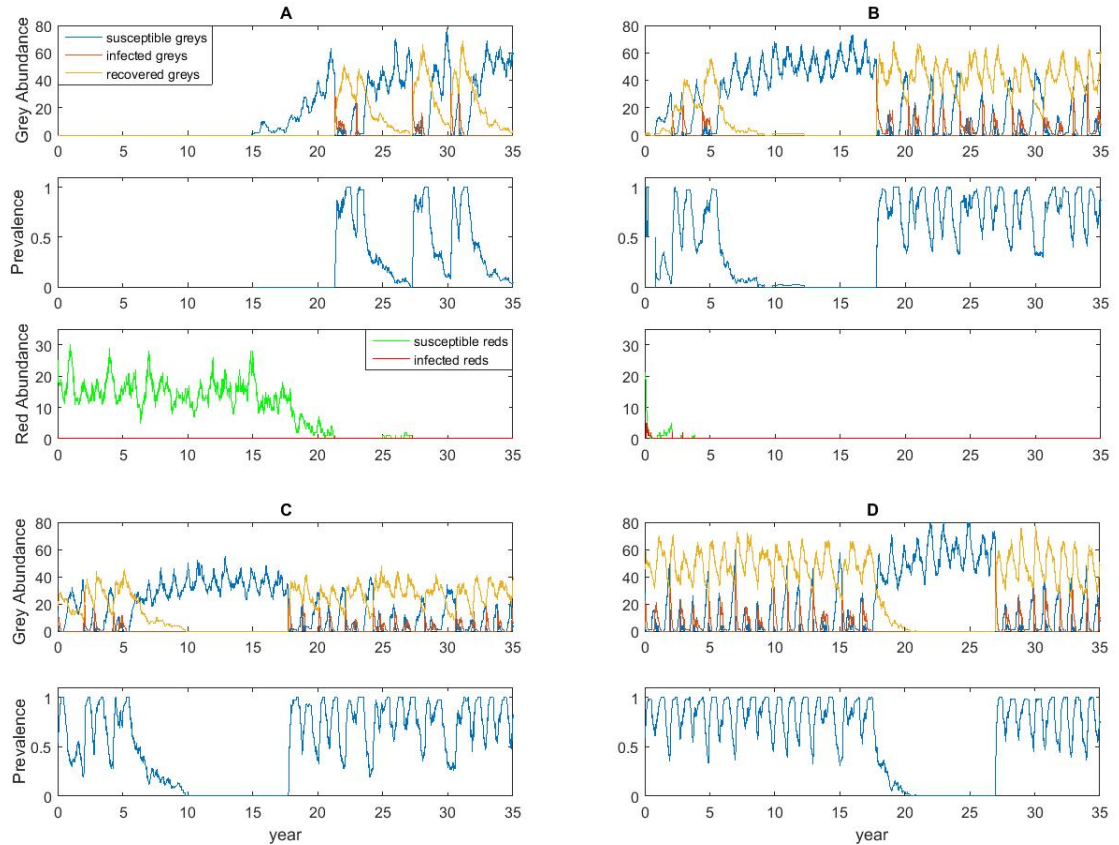


Figure 3.7: Population abundance and prevalence of sero-positive grey squirrels between years 0 and 35 in the cells highlighted by the labelled circles in Figure 3.5. In (A) and (B) the population abundance of susceptible and infected red squirrels is also plotted.

3.6 Discussion

We developed a spatial, stochastic model of red-grey-squirrelepox dynamics on Anglesey and showed how the model could represent the historical replacement of red by grey squirrels observed from 1966 to 1998. If the initial invasion of grey squirrels on Anglesey includes individuals that carry SQPV this can lead to a local disease outbreak in red squirrels in the relatively high density populations in regions adjacent to the Britannia Bridge. In these (localised) regions, competition and disease processes led to the rapid replacement of red squirrels by grey squirrels. The fragmented nature of the habitat on Anglesey, where the majority of habitat on the island supports only low density squirrel populations, coupled with the high virulence of SQPV in red squirrels, means the infection failed to spread extensively via intra-specific pathways through the resident native red squirrel populations on Anglesey. Squirrelepox also failed to persist in establishing grey squirrel populations on Anglesey and therefore, SQPV was absent from Anglesey for a significant period while the grey squirrel range expanded. During this period, competition was the key driver of grey squirrel invasion and establishment. Once the grey squirrel abundance and range had increased on Anglesey, squirrelepox could establish and persist, with reinfection driven through grey squirrel intra-specific pathways with populations on the mainland. By this time, many of the red squirrel populations on Anglesey had been replaced by grey squirrels, with the impact of squirrelepox on red squirrels limited to localised outbreaks at the leading edge of the expanding grey distribution. The model findings suggest that squirrelepox may not play a significant role in the invasion of grey squirrels and replacement of red squirrels when they occupy habitats that predominantly support relatively low population densities.

An important finding in our study - that squirrelepox is not always a key factor in the invasion of grey squirrels into landscape occupied by red squirrels - qualifies previous studies that had suggested that the presence of the infection will (automatically) significantly increase the rate of red squirrel replacement by grey squirrels (Tompkins et al., 2003; Rushton et al., 2006; Bell et al., 2009; White et al., 2014). The previous studies suggest that the infection and associated disease will spread through red squirrel populations in advance of invading grey squirrels, causing red squirrel population crashes, with the resultant low red squirrel population density offering little competitive resistance to incursion and population establishment of the advancing grey squirrels. It is noteworthy, that previous studies have typically represented systems that can support high density red populations; for example densities of 2.5 to 4.0 squirrels per ha in a designated stronghold in Formby, Lancashire. In such examples, intra-specific squirrelepox infection can lead to epidemics in red squirrels resulting in 80% mortality (Chantrey et al., 2014; White et al., 2014). In

systems with lower densities, such as 0.5 to 0.8 per ha reported within Dumfries and Galloway, models indicate that populations suffer less severe epidemics with 60% mortality (White and Lurz, 2014; White et al., 2016a).

The model findings presented here for the Anglesey system represents habitat that is fragmented, modelled using one km cells supporting approximately 0.05 to 0.25 red squirrels per hectare. The results indicate that squirrelpox can spread at a localised level within fragmented habitats that support higher red squirrel densities, but here the disease will fade-out and fail to persist. Moreover, squirrelpox was not predicted to spread extensively across Anglesey as it failed to spread throughout the predominantly low density landscape that connected fragments of better quality habitat. This reinforces previous model findings that examined squirrelpox spread at low density (White et al., 2014; Macpherson et al., 2016a). Since squirrelpox fails to spread through the established red squirrel populations, it does not lead to the widespread disease induced mortality that reduces red squirrel density, nor the subsequent advantage to grey squirrels through disease mediated invasion. In low density environments, the model predicts that competitive processes are the key drivers of the replacement of red squirrels by grey squirrels.

Control measures implemented in the period 1998 to 2013 led to the eradication of grey squirrels from Anglesey (Shuttleworth et al., 2015a) and in the period 2004 to 2013, red squirrels were reintroduced to many parts of the island with the result that it supports a population of approximately 700 red squirrels (Halliwell et al., 2015). Histological tests have shown that even though restored red squirrel populations were sympatric with grey squirrels during some periods, no squirrelpox disease was recorded in red squirrels and no animals were ever found with antibodies to SQPV (Shuttleworth et al., 2015b). This is likely due to the impact of grey squirrel control reducing grey squirrel density to levels that could not support squirrelpox in regions where red and grey squirrels were sympatric (Schuchert et al., 2014). However, with the close proximity of a mainland grey squirrel population and dispersal opportunities offered by the Britannia Bridge, it is unsurprising that since eradication, a small number of re-incursion events have been recorded (Shuttleworth, 2016). A concern of conservation groups is that such incursions may introduce squirrelpox to the re-established red squirrel island population. Our work suggests that if this happened, squirrelpox disease outbreaks in red squirrels would be localised and the infection would fade-out (Figure 3.6). While localised outbreaks would cause red squirrel mortality, provided grey squirrels are prevented from establishing on the island, the red squirrel population will return to pre-infection densities following disease fade-out. A caveat to our findings, is that the model assumes the same rate of transmission for grey-grey, grey-red, red-grey and red-red squirrel interactions. Since red squirrel infections are more acute/symptomatic, it may be that

red squirrels have a higher level of infectivity. In particular, if the rate of transmission between red squirrels is increased (beyond the current level that is fitted for grey-grey transmission), then the disease can spread more extensively and cause greater levels of mortality, although it is still predicted to fade-out after an epidemic outbreak (Macpherson et al., 2016a).

Our modelling work may help explain the epidemiological dynamics of SQPV in grey squirrel populations. Model results examining the sero-prevalence of SQPV in grey squirrel populations as their range expanded on Anglesey indicate that the infection failed to persist in grey squirrel populations and therefore the sero-prevalence was low or zero, until their abundance and range had expanded. Field observations support this finding reporting low sero-prevalence at the wave-front of grey squirrel expansion in Ireland where population levels are low (Stritch et al., 2015). Model results also highlight that there can be considerable variation in the levels of prevalence both annually and on a multi-year level. The annual signal shows that prevalence is driven by the seasonal pattern of reproduction, with a peak at the end of the breeding season. However, the model findings indicate that in addition to the annual signal, prevalence can become low or SQPV can fade-out periodically before being reintroduced through dispersal (Figure 3.7). The fade-out of SQPV in grey squirrel populations occurs at the regional scale in the model with low or zero sero-prevalence in the connected region around Bangor between years 10 to 18 (Figure 3.5, Figure 3.7C) and in the Gwydir forest park region around Betws-y-Coed between years 20 to 27 (Figure 3.5, Fig 3.7D). SQPV becomes re-established through the rare dispersal of infected individuals between regions. This has important implications for disease monitoring in the field as variation in the sero-prevalence in grey squirrel populations may depend on the time of year in which sampling is undertaken, on the population abundance in a particular year (which will depend on seed availability), or on the size and level of connectivity of a particular forest block as infection may periodically fade out at the regional level. Importantly, our work indicates that the significant and sustained reduction in grey squirrel density, through control, is likely to reduce SQPV prevalence in grey squirrels - this is supported by field studies (Schuchert et al., 2014).

The findings in this study, have shown how mathematical models can be useful tools for understanding the key population and disease processes involved in ecological invasions and for informing conservation management practice. Future work will focus on extending the models to represent the control of grey squirrels and to fit the model to the population data on Anglesey between 1998 and 2013, in which grey squirrels were removed and red squirrels reintroduced and established. This model can help plan future conservation decisions on Anglesey and on the neighbouring mainland and can be adapted to inform on red squirrel conservation

strategy throughout the UK.

3.7 Acknowledgements

AW, MB and PL are supported in part by a NERC Innovations grant NE/M021319/1. HEJ is supported by an EPSRC DTA award and funding via a Heritage Lottery Fund grant award. The authors would like to thank Jonathan Rothwell and Dr Liz Halliwell of Natural Resources Wales, for providing GIS Land Cover Map layers and two anonymous referees for detailed and helpful comments.

3.A Assessing the impact of seasonal growth on the epidemiological dynamics in the deterministic model.

3.A.1 Non-seasonal deterministic model

First we consider the non-seasonal deterministic model of the red/grey/squirrelepox system, Equations 3.A.1-3.A.5, as described by Tompkins et al. (2003) (also see White et al. (2014)).

$$\frac{\partial S_G}{\partial t} = a_G (1 - q_G(H_G + c_R H_R)) H_G - b S_G - \beta S_G(I_G + I_R) \quad (3.A.1)$$

$$\frac{\partial I_G}{\partial t} = \beta S_G(I_G + I_R) - b I_G - \gamma I_G \quad (3.A.2)$$

$$\frac{\partial R_G}{\partial t} = \gamma I_G - b R_G \quad (3.A.3)$$

$$\frac{\partial S_R}{\partial t} = a_R (1 - q_R(H_R + c_G H_G)) H_R - b S_R - \beta S_R(I_G + I_R) \quad (3.A.4)$$

$$\frac{\partial I_R}{\partial t} = \beta S_R(I_G + I_R) - b I_R - \alpha I_R \quad (3.A.5)$$

Here, the reproductive rate, a is a constant that operates continuously. The maximum reproductive rate is modified due to intra and inter specific competition and the crowding term q is set such that the separate species achieve their carrying capacity in the absence of the other species and squirrelepox.

For the non-seasonal model, the single species equation is:

$$\frac{dN}{dt} = aN(1 - qN) - bN \quad (3.A.6)$$

To determine the value of q , we solve at the steady state and equate this to the

carrying capacity, K .

$$\text{For steady states, } \frac{dN}{dt} = 0 \quad (3.A.7)$$

$$\text{therefore } \frac{dN}{dt} = aN(1 - qN) - bN = 0 \quad (3.A.8)$$

$$N = 0 \quad \text{or} \quad a(1 - qN) - b = 0 \quad (3.A.9)$$

$$\Rightarrow N = \frac{a - b}{aq} = K \quad (3.A.10)$$

Therefore q can be set for each species as $q_R = \frac{a_R - b}{a_R K_R}$ and $q_G = \frac{a_G - b}{a_G K_G}$.

3.A.2 Seasonal deterministic model

The model considered in the main text in this study (Equations 3.2-3.5) is a modification of Equations 3.A.1-3.A.5 that assumes that reproduction is seasonal (with birth occurring for 6 months between March and September only). This seasonal reproduction means that the population density oscillates throughout the year with a clear annual signal with density peaking at the end of the breeding season. We wish to fit the parameters in the model such that the carrying capacity for each species equates to the average annual density. The following calculation explains how the crowding term q is set to achieve this.

The seasonal model (comparable to Equation 3.A.6 in the non-seasonal case) where birth occurs for a fraction $1/s$ of the season is given by

$$\frac{dN}{dt} = asN(1 - qN) - bN \quad 0 < t < \frac{1}{s} \quad (3.A.11)$$

$$= -bN \quad \frac{1}{s} \leq t < 1 \quad (3.A.12)$$

Note that the maximum birth rate a is multiplied by s to ensure that the annual birth rates for models with different season durations is equivalent. Equation 3.A.11 can be written as follows

$$\frac{dN}{dt} = N(C - DN) \quad \text{where} \quad C = as - b, \quad D = asq \quad (3.A.13)$$

We can solve this differential equation as follows

$$\Rightarrow \int \frac{1}{N} + \frac{D}{C - DN} dN = \int C dt \quad (3.A.14)$$

$$\frac{N}{C - DN} = Ae^{Ct} \quad (3.A.15)$$

Assuming the initial condition $N(0) = N_0$ we can find the constant $A = \frac{N_0}{C - DN_0}$. Therefore the density at the end of the breeding season is

$$N(1/s) = N_s = \frac{CAe^{\frac{C}{s}}}{1 + DAe^{\frac{C}{s}}} \quad (3.A.16)$$

Secondly, solving Equation 3.A.12 we find,

$$N = Be^{-bt} \quad (3.A.17)$$

and using the condition for $N(1/s)$ we find that

$$N = N_s e^{-b(t - \frac{1}{s})} \quad (3.A.18)$$

Therefore at the end of the non-breeding season, the density is

$$N(1) = N_s e^{-b(1 - \frac{1}{s})} \quad (3.A.19)$$

For a periodic solution, we require that $N(0) = N(1)$. Using Equation 3.A.19 implies that

$$N_0 = N_s e^{-b(1 - \frac{1}{s})} \quad (3.A.20)$$

Substituting N_s given by Equation 3.A.16 gives

$$N_0 = \frac{CAe^{Ct}}{1 + DAe^{Ct}} e^{-b(1-t)} \quad (3.A.21)$$

$$\text{therefore } N_0 = \frac{CN_0 e^{-b(1-t)}}{(C - DN_0)(1 + \frac{DN_0 e^t}{C - DN_0})} \quad (3.A.22)$$

$$\text{which can be rearranged as } N_0 = \frac{C(e^{\frac{-b(s-1)}{s}} \cdot e^{\frac{C}{s}} - 1)}{D(e^{\frac{C}{s}} - 1)} \quad (3.A.23)$$

The average density over period can be calculated as:

$$N_{av} = \int_0^{\frac{1}{s}} \frac{CAe^{Ct}}{1 + DAe^{Ct}} dt + \int_{\frac{1}{s}}^1 N_s e^{-b(t-\frac{1}{s})} dt \quad (3.A.24)$$

$$= \left[\frac{1}{D} \ln(1 + DAe^{Ct}) \right]_0^{\frac{1}{s}} + \left[\frac{-N_s}{b} e^{-b(t-\frac{1}{s})} \right]_{\frac{1}{s}}^1 \quad (3.A.25)$$

$$= \frac{1}{D} \ln \left(\frac{1 + DAe^{\frac{C}{s}}}{1 + DA} \right) + \frac{N_s}{b} \left(1 - e^{-b(1-\frac{1}{s})} \right) \quad (3.A.26)$$

and this can be simplified (with the help of Maple) to

$$N_{av} = \frac{1}{D} \left[\left(\frac{C + b - bs}{s} \right) + \frac{C(e^{\frac{C+b-bs}{s}} - 1)e^{\frac{b(s-1)}{s}} \left(1 - e^{-\frac{b(s-1)}{s}} \right)}{b \left(e^{\frac{C}{s}} - 1 \right)} \right] \quad (3.A.27)$$

$$= \frac{1}{D} [\phi] \quad (3.A.28)$$

We wish to equate N_{av} with the carrying capacity, therefore

$$K = \frac{1}{asq} [\phi] \quad (3.A.29)$$

This allows us to set q as

$$q = \frac{1}{asK} [\phi] \quad (3.A.30)$$

Note when $s = 1$ and therefore birth is continuous, we recover N_{av} .

$$\frac{C}{D} = \frac{as - b}{asq} \quad (3.A.31)$$

$$\text{and therefore } q = \frac{a - b}{asK} \text{ as in Equation 3.A.10.}$$

In our study, we assume a six month breeding season so we set $s = 2$ in Equation 3.A.30.

3.A.3 Numerical solutions of deterministic equations

Using ode45 in Matlab, the non-seasonal and seasonal deterministic equations were solved numerically to compare the non-seasonal model from Tompkins et al. (2003) with the adapted seasonal version. The disease-free single species models show how the population density in the season model oscillates with an annual signal around the carrying capacity (Figures 3.A.1 and 3.A.2).

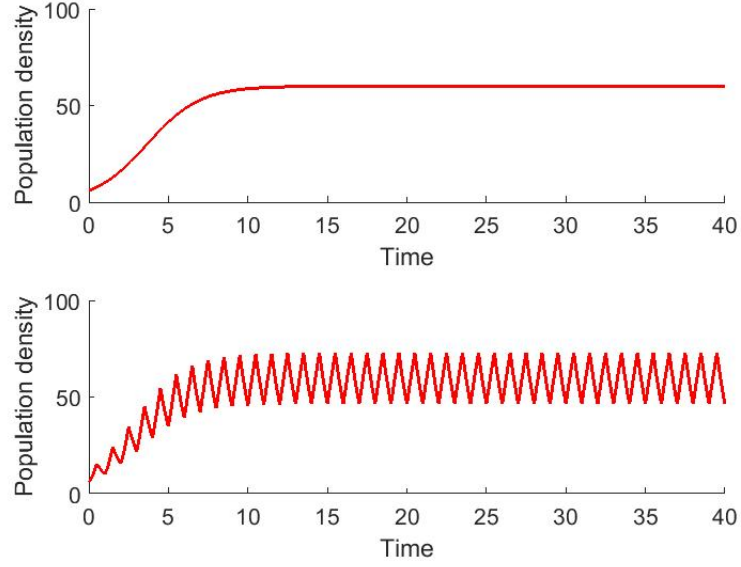


Figure 3.A.1: The population dynamics for the red squirrel only disease-free system for the non-seasonal (Equations 3.A.4-3.A.5) (top) and seasonal (Equations 3.4-3.5) (bottom) cases in which $K_R = 60$ with initially 10% of the carrying capacity present. Other parameters are as detailed in the main text (Section 3.4.2).

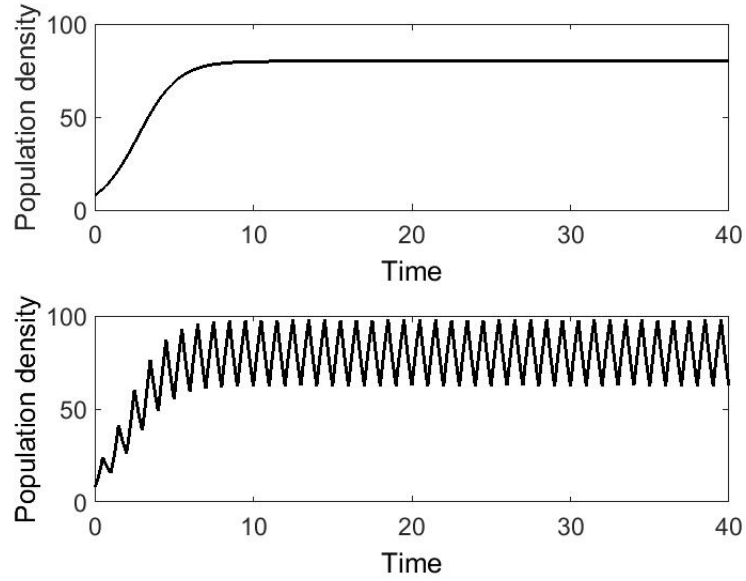


Figure 3.A.2: The population dynamics for the grey squirrel only disease-free system for the non-seasonal (Equations 3.A.1-3.A.3) (top) and seasonal (Equations 3.2-3.3) (bottom) cases in which $K_G = 80$ with initially 10% of the carrying capacity present. Other parameters are as detailed in the main text (Section 3.4.2).

The results that highlight disease-mediated invasion are similar in the non-seasonal (Equations 3.A.1-3.A.5) and seasonal (Equations 3.2-3.5) model, (Figure

3.A.3). The difference is that there is a clear annual signal to the population dynamics in the seasonal model. The results show that there is an initial epidemic in the red population, which reduces the competitive pressure on greys and allows them to grow more rapidly. This supports the disease and leads to a second population crash in the red population and the replacement of red squirrels with 6 years.

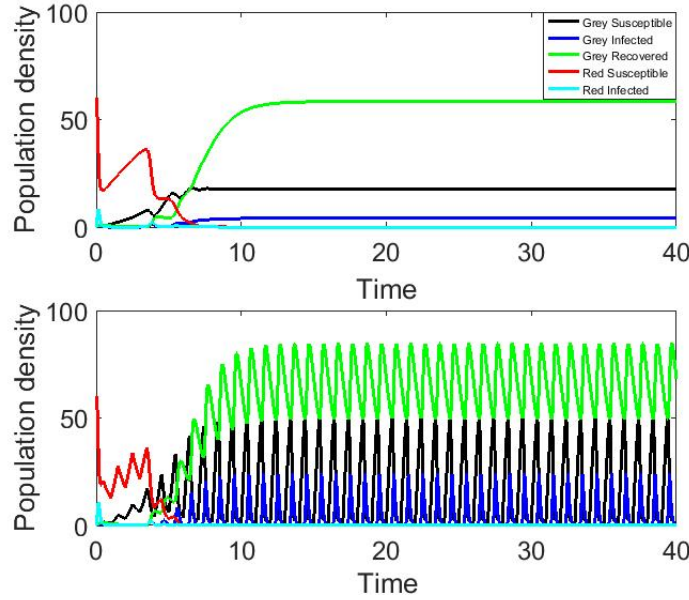


Figure 3.A.3: The population dynamics of the non-seasonal (Equations 3.A.1-3.A.5)) (top) and seasonal (Equations 3.2-3.5) (bottom) cases when one infected grey squirrel is introduced into a purely susceptible red squirrel population at its carrying capacity ($K_R = 60$ and $K_G = 80$). Parameters are as detailed in the main text (Section 3.4.2) except from a in the non-seasonal system in which $a_R = 1.5$ and $a_G = 1.7$.

3.B Dispersal

We use the data on the replacement of red squirrels by greys on Anglesey to parametrise the dispersal parameters in the model. In particular we wish to examine the parameter sets that lead to the expansion of grey squirrels over most of the island and the replacement of red squirrels within 35 years of greys' occurrence on Anglesey. We consider a range of values of the dispersal rate (m) and the maximum dispersal distance. In Figure 3.B.4, we see that a value of $m = 2b = 1.8$ and the maximum dispersal distance of 2km gave the best match with the observed data, with greys colonising most of the island within the observed 35 years of introduction and only a few reds remaining in the north west of the island.

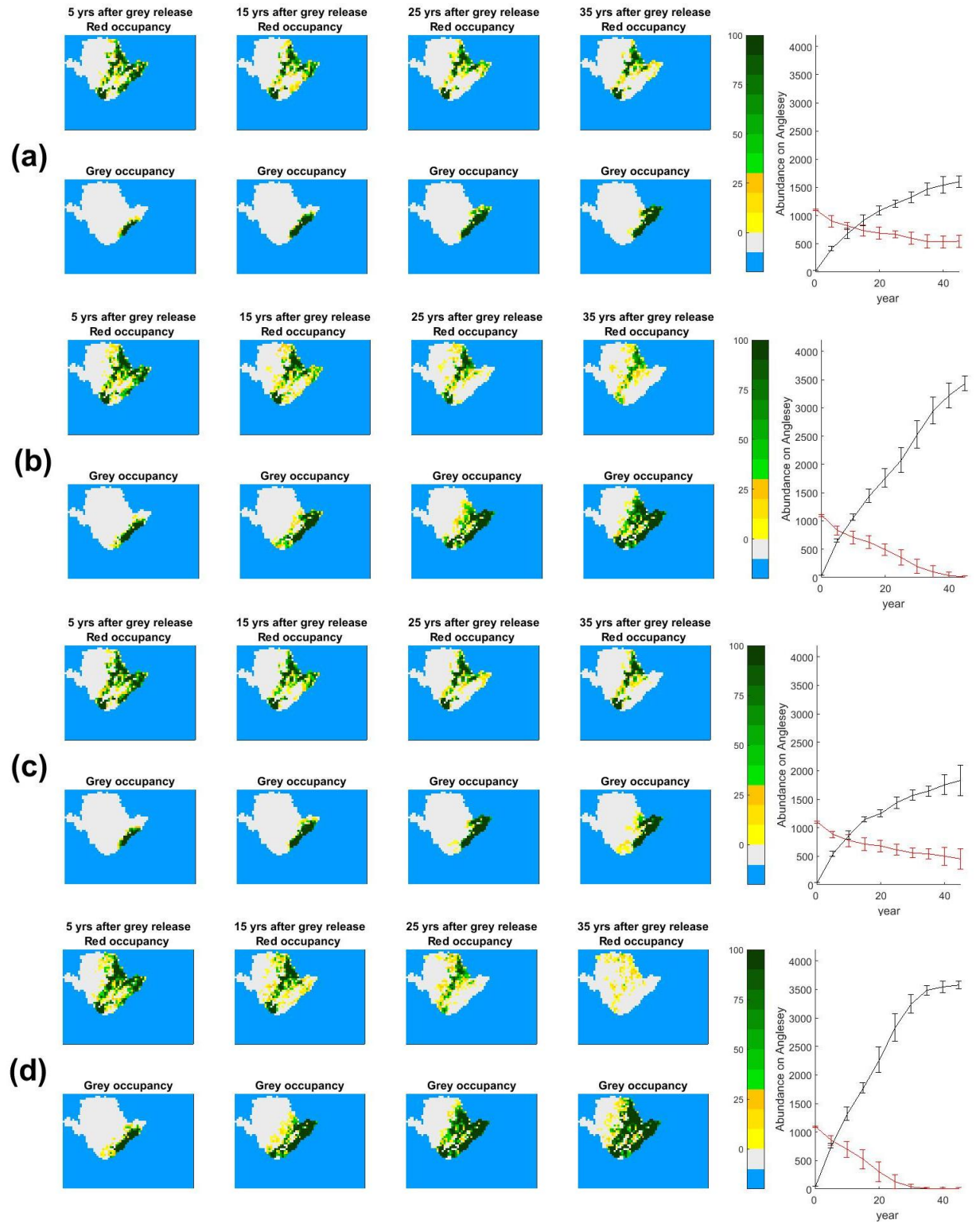


Figure 3.B.4: The percentage occupancy of red and grey squirrels on Anglesey and the average population abundance across 20 realisations over time (with 95% confidence intervals). The model is initialised by running the model with just red squirrels for 25 years as a spin-up phase and then introducing 25 grey squirrels in a grid square on Anglesey adjacent to the Britannia Bridge. The parameters are (a) maximum dispersal = 1km, $m=b$; (b) maximum dispersal = 2km, $m=b$; (c) maximum dispersal = 1km, $m=2b$; (d) maximum dispersal = 2km, $m=2b$. Other parameters are given in the main text in Section 3.4.2.

Chapter 4

Mathematical models of invasive species management: Grey squirrel control on Anglesey

The following chapter is based on a paper currently being published in the journal *Ecological Modelling*. I did the modelling within it and wrote the paper with help from the co-authors (Andy White, Peter Lurz and Craig Shuttleworth). Additional work on the topic outwith the content of the paper has been included and immediately follows the discussion. Additional information supporting the paper has been included in an appendix at the end of this chapter.

4.1 Abstract

The control of invasive species and protection of threatened native species requires well-developed policy and species management strategies. Mathematical models provide a key tool that can be used to test, develop and optimise strategies to manage invasive species. We use the native red squirrel and invasive grey squirrel system on the Isle of Anglesey, UK, as a case study system in which to parameterise a mathematical model that includes the control of grey squirrels. We develop a stochastic, spatial model that represents the real habitat structure, distribution and linkage on Anglesey and the neighbouring mainland and includes the key population and epidemiological dynamics of the red-grey-squirrelepox system. The model also includes a representation of the trapping and removal of grey squirrels which is parameterised from field data on Anglesey in which grey squirrels were removed and red squirrels reintroduced between 1998-2013. The model is used to assess different management procedures to protect red squirrels from island re-invasion by grey squirrels; including the threat of squirrelepox spread posed by endemic mainland grey populations.

The findings have important implications for the conservation of threatened red squirrels throughout the UK and in Europe. Moreover, the modelling framework is based on well-understood, classical models of competitive and epidemiological interactions and therefore the techniques can be adapted and applied more generally to manage the threat of invasive species in a wide range of natural systems.

4.2 Introduction

The redistribution of organisms, either accidentally, deliberately or because of environmental change, is causing an invasive threat to native species diversity at the global scale (Ehrenfeld, 2011; Kolar and Lodge, 2001; Mack et al., 2000; Manchester and Bullock, 2000; Martin-Albarracin et al., 2015; Simberloff, 2011). In many cases the impacts of invading species are not considered until the problem is severe and then extensive intervention is required to limit the impacts or eradicate the invader, (Mack et al., 2000). Early intervention is the most cost effective and successful strategy to limit the impact of invasive species, (Hulme, 2006; Manchester and Bullock, 2000), requiring well-developed contingency strategies that can be invoked at the onset of invasion (Manchester and Bullock, 2000).

The eradication of invasive species is often required to protect native species. For example, the muskrat (*Ondatra zibethicus*) was successfully eradicated from the UK in the 1930s. Here, the negative effects of muskrats on agriculture observed in continental Europe led to early intervention in the UK and population control was undertaken before the muskrat could spread extensively (Gosling and Baker, 1989; Manchester and Bullock, 2000). However, eradication attempts in the past have not always been successful, resulting in detrimental impacts to native biodiversity (Mack et al., 2000). For example, the eradication of the coypu (*Myocastor coypus*) from the UK initially failed. The invasive threat posed by coypus was initially underestimated and allowed populations to increase in density and spread (Gosling and Baker, 1989). Following the failure of the first eradication campaign (1962-1965), extensive preliminary investigation into coypu population biology was used to provide a detailed control strategy and an assessment of the likelihood of successful eradication (Gosling and Baker, 1989). Mathematical modelling was used to determine the optimal trapping procedure, with the procedure modified in response to data gathered from control on the ground (Gosling and Baker, 1989; Manchester and Bullock, 2000). The combination of preliminary planning, modelling and responsive adjustments to the control scheme led to the eradication of the coypu within 8 years (Gosling and Baker, 1989). This highlights how an assessment of the population biology combined with population modelling is important to ensure eradication is efficient and successful (Bonesi et al., 2007). In this study we use

population modelling techniques to aid the management of invasive grey squirrel control in the UK.

The replacement of the native red squirrel (*Sciurus vulgaris*) by the North American grey squirrel (*S. carolinensis*) in the UK is an example of disease-mediated ecological invasion. Grey squirrels are abundant throughout most of the UK having replaced red squirrels in the majority of England and Wales and in parts of southern Scotland (Bryce, 1997; Gurnell et al., 2004; Halliwell et al., 2015; O'Teangana et al., 2000). The remaining widespread red squirrel populations are in northern Scotland, along with often fragmented populations, typically sympatric with grey squirrels, in southern and central Scotland, northern England and Wales (Halliwell et al., 2015). Preventing further grey squirrel population expansion and removing sympatric grey squirrels are major priorities in conserving the remaining red squirrel populations (DEFRA, 2007; Forestry Commission Scotland, 2012; Forum, 2009; Parrott et al., 2009; Schuchert et al., 2014). Grey squirrels out compete red squirrels in many habitats and also carry squirrelpox - an asymptomatic infection harmless to grey squirrels that produces pathological disease in red squirrels (McInnes et al., 2006; Sainsbury et al., 2008).

Mathematical models have highlighted the potential of grey control to protect red populations and to prevent the spread of squirrelpox, (White et al., 2014, 2016a), but to date have not been able to provide detailed grey squirrel control strategies, instead focusing on hypothetical control (or reduced fecundity) scenarios (e.g Rush-ton et al. (2002)). However, one of the questions posed by red squirrel conservation organisations is 'where and how much control' is required to protect remaining key red squirrel populations. While mathematical modelling can be used to inform on this question, up to now it has been limited by a lack of suitable data from which to parameterise the model (particularly in terms of the initial distribution and density of red and grey squirrels in regions where grey squirrel control has been undertaken). The 710km² Isle of Anglesey located off the coast of north-west Wales (see Figure 3.1) provides a case study region in which a mathematical model of grey squirrel control can be parameterised and thereby provide a tool that can be used to develop red squirrel conservation strategies to protect red squirrels throughout the UK.

Until the 1960s, red squirrels were the only squirrel species that inhabited Anglesey (Walker, 1968). However, the grey squirrel was expanding its range across the UK and they were recorded moving west along the north Wales coast, reaching Flintshire and Denbighshire (1945-1952), before being recorded in Caernarvonshire (Gwynedd) in the late 1950s (Shorten, 1954). The first grey squirrels were reported on Anglesey in 1966 (Walker, 1968), though potentially grey squirrels dispersed to the island prior to this. Two bridges, the Britannia Bridge (1850/1972) and the Menai Bridge (1826) connect the island to the mainland with the former being

thought to be the primary route squirrels use to enter and leave the island (Schuchert et al., 2014) (see Figure 3.1). Suitable habitat for squirrels extends to the waterfront on either side of the Britannia Bridge with the lower level providing a clear dispersal corridor as it is used infrequently by trains. From c. 1966, grey squirrels established and spread on the island, reaching an abundance of 3000-4000 by 1998 (Halliwell et al., 2015) and almost completely replacing red squirrels (with approximately 40 red squirrels remaining on Anglesey by 1998 (Shuttleworth, 2003)). Grey squirrel control measures were implemented from 1998 and led to the eradication of grey squirrels from Anglesey by 2013 (Shuttleworth et al., 2015a). Moreover, in the period 2004-2013, red squirrels were reintroduced to many parts of the island with the result that it supports a population of approximately 700 red squirrels (in 2015) (Halliwell et al., 2015). The island of Anglesey therefore provides a unique case study system from which to parameterise key squirrel life history parameters and to model the control of grey squirrels. In particular, the key population data of red squirrels at their carrying capacity in 1966 (with no grey squirrels) and grey squirrels at their carrying capacity in 1998 (with few red squirrels) allows the dispersal and invasive replacement of reds by greys to be modelled. The well-documented removal of grey squirrels through trapping by 2013 (Schuchert et al., 2014) allows key grey squirrel control processes to be modelled.

A key aim of this study is to develop a mathematical model that includes the control of grey squirrels on Anglesey. This model can then be used to assess different management procedures that will protect red squirrels from island re-invasion by grey squirrels; including the threat of squirrelpox spread posed by mainland grey populations. Anglesey contains fragmented woodlands that support low/medium densities of red squirrels, and is therefore similar habitat to that found within many of the remaining geographical red squirrel stronghold areas elsewhere in the UK. Consequently, the findings will have wider implications for the conservation of red squirrels throughout the UK (and elsewhere in Europe where grey squirrel invasion is also leading to the replacement of native red squirrels (Martinoli et al., 2010; Wauters et al., 2005)). Moreover, the modelling framework developed in this study is based on well-understood, classical models of competitive and epidemiological interactions (Tompkins et al., 2003). The techniques, therefore, can be adapted and applied more generally to manage the threat of invasive species in a wide range of natural systems.

4.3 Methods

The overall modelling framework represents the abundance of red and grey squirrels and squirrelpox infection status in 1 km by 1 km grid squares. Grid squares are

linked by dispersal and the potential squirrel density in each grid square is based on landcover data that approximates the real heterogeneous habitat of Anglesey.

4.3.1 A Mathematical Model of the Anglesey Squirrel System

Calculating Potential Squirrel Abundance Using GRASS GIS software (GRASS Development Team, 2016), we used digital landcover maps supplied by Natural Resources Wales to extract the dominant habitat type at a 25 m by 25 m scale for Anglesey and the adjacent mainland. This data was combined with estimates of squirrel densities in different habitat types (Table 4.1) and summed to obtain the potential density of red and grey squirrels at a 1 km x 1 km patch level (this scale has been used successfully to model the UK squirrel system in previous studies, (Macpherson et al., 2016a; White et al., 2014, 2016a)). When these estimates are combined with the model (see below) they predict that Anglesey can support approximately 4000 grey squirrels and 1000 red squirrels (Figure 4.1) which is in good agreement with field estimates (Halliwell et al., 2015; Schuchert et al., 2014).

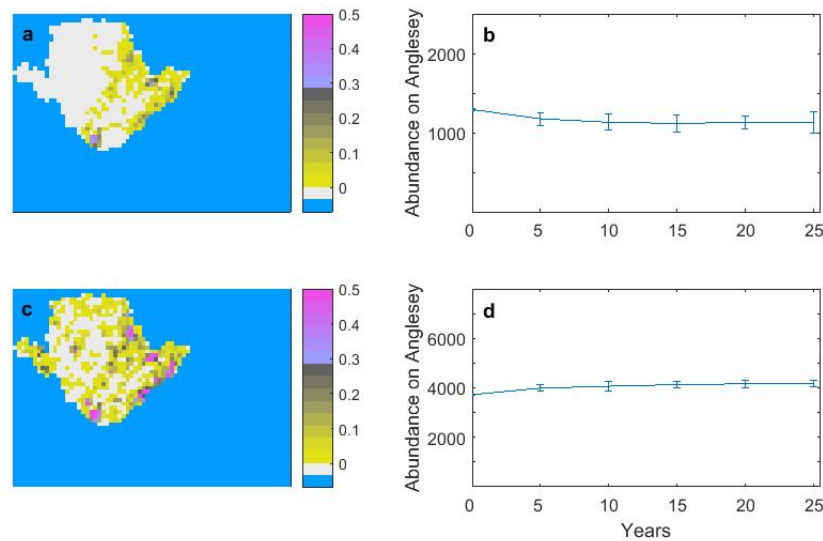


Figure 4.1: A map of the density (/ha) of (a) red squirrels and (c) grey squirrels on Anglesey after 25 years for a single model realisation using the estimates of potential density shown in Table 4.1 (the colour bar indicates squirrel density per hectare which is determined by dividing the number of squirrels in each 1 km by 1 km cell by 100). The graphs in (b) and (d) show the change in average abundance for red and grey squirrels over a 25 year time period for 20 model realisations (with 95% confidence intervals).

Table 4.1: Estimates of squirrel densities per hectare for the different habitats recorded in the landcover data on Anglesey and neighbouring mainland, taken from the following sources: Bosch and Lurz (2012); Gurnell (1983, 1996a).

Habitat	Red squirrels (/ha)	Grey squirrels (/ha)
semi-natural broadleaved woodland	0.65	2.50
planted broadleaved woodland	0.65	2.50
semi-natural coniferous woodland	0.35	0.6
planted coniferous woodland	0.35	0.6
semi-natural mixed woodland	0.65	1.25
planted mixed woodland	0.65	1.25
dense scrub	0.25	0.65
introduced scrub	0.25	0.65
gardens	0.315	0.94
caravan site	0.16	0.47

The model framework We base our model framework on previous mathematical models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al., 2003) to consider a spatial, stochastic model of the red/grey/squirrelepox system, (Macpherson et al., 2016a; White and Lurz, 2014; White et al., 2014, 2016b). Here, the deterministic underpinning allows the key population dynamical processes to be understood (Tompkins et al., 2003) and the stochastic adaptation provides essential realism when squirrel numbers become low and therefore the chance of extinction and the fade-out of infection is represented. The stochastic model is developed by modifying the deterministic system of (Tompkins et al., 2003) which represents the population densities of susceptible and infected reds (S_R , I_R) and susceptible, infected and immune greys (S_G , I_G , R_G) at time t , in years, in each 1 km by 1 km grid cell. The underlying

deterministic model is as follows:

$$\frac{dS_G}{dt} = A_G(t) - bS_G - \beta S_G(I_G + I_R) \quad (4.1)$$

$$\frac{dI_G}{dt} = \beta S_G(I_G + I_R) - bI_G - \gamma I_G \quad (4.2)$$

$$\frac{dR_G}{dt} = \gamma I_G - bR_G \quad (4.3)$$

$$\frac{dS_R}{dt} = A_R(t) - bS_R - \beta S_R(I_G + I_R) \quad (4.4)$$

$$\frac{dI_R}{dt} = \beta S_R(I_G + I_R) - bI_R - \alpha I_R \quad (4.5)$$

where $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total squirrel populations and

$$\text{where } A_G(t) = \begin{cases} a_G (1 - q_G(H_G + c_R H_R)) H_G & t_n \leq t < t_{n+1} + 0.5 \\ 0 & t_n + 0.5 \leq t < t_{n+1} \end{cases}$$

represents the periodic birth rate of grey squirrels assuming births occur during six months of the year (March - September). The term for $A_R(t)$ is equivalent to $A_G(t)$ with the subscripts for R and G interchanged. This seasonality in reproduction causes the population density to exhibit annual oscillations around the potential density. Towards the end of the breeding season, the population density is above the potential density, triggering an increase in squirrel dispersal as is observed in the natural system, (see Chapter 3, Macpherson (2014)). All other life-history and disease processes occur throughout the year. The species have the same rate of adult mortality ($b = 0.9$, (Barkalow et al., 1970; Tompkins et al., 2003)) but different rates of maximum reproduction ($a_G = 3.4$, $a_R = 3.0$, (Tompkins et al., 2003), adjusted to account for seasonality). The competitive effect of grey squirrels on red squirrel is $c_G = 1.65$ and red squirrels on grey squirrels is $c_R = 0.61$, (Bryce, 1997). The transmission rate of squirrelpox virus between and within each species is $\beta = 3.27$ obtained by matching the sero-prevalence on the mainland adjacent to Anglesey of 67% (Jones et al., 2016; Schuchert et al., 2014; Tompkins et al., 2003). Death due to the disease occurs in infected red squirrels at rate $\alpha = 26$ and infected grey squirrels recover at rate $\gamma = 13$, (Tompkins et al., 2003). The susceptibilities to crowding (q_R , q_G) are set to ensure that the average density over one year is equal to the potential density in each grid square.

To generate the stochastic model, the rates in the deterministic model are con-

verted to probabilities of events that account for changes in individual grid cell level abundance (Renshaw, 1991). The probabilities are given in Table 4.2.

Table 4.2: The stochastic model within each 1 km by 1 km grid square indicating the probability of different events. Here $R = \sum[\text{rates}]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (and are set to zero otherwise). Transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells due to daily movement within a core range of radius, $\theta = 0.15\text{km}$. The dispersal term is shown for the class S_G only but is similar for all other classes. The model assumes density dependent dispersal such that squirrel dispersal increases as density increases and the dispersal rate is $m = 2b$ when the patch density is equal to the potential density. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of 2 km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). The dispersal parameter values were set by comparing model results and field data for the expansion of grey squirrels and replacement of red squirrels on Anglesey between 1966 and 1998 (see Chapter 3).

Birth of Grey to S_G	$P(S_G \rightarrow S_G + 1)$	$:[(a_G - q_G(H_G + c_R H_R)) H_G]/R$
Natural Death of S_G	$P(S_G \rightarrow S_G - 1)$	$:[b S_G]/R$
Infection of Grey	$P(S_G \rightarrow S_G - 1, I_G \rightarrow I_G + 1)$	$:[\beta S_G(I_G + I_R)]/R +$ $+ \theta \sum_{\text{Adjacent}} (I_G + I_R) +$ $+ \theta^2 \sum_{\text{Corner}} (I_G + I_R)]/R$
Natural death of I_G	$P(I_G \rightarrow I_G - 1)$	$:[b I_G]/R$
Recovery of Grey	$P(I_G \rightarrow I_G - 1, R_G \rightarrow R_G + 1)$	$:[\gamma_G I_G]/R$
Natural Death of R_G	$P(R_G \rightarrow R_G - 1)$	$:[b R_G]/R$
Birth of Red to S_R	$P(S_R \rightarrow S_R + 1)$	$:[(a_R - q_R(H_R + c_G H_G)) H_R]/R$
Natural Death of S_R	$P(S_R \rightarrow S_R - 1)$	$:[b S_R]/R$
Infection of Red	$P(S_R \rightarrow S_R - 1, I_R \rightarrow I_R + 1)$	$:[\beta S_R((I_G + I_R) +$ $+ \theta \sum_{\text{Adjacent}} (I_G + I_R) +$ $+ \theta^2 \sum_{\text{Corner}} (I_G + I_R)]/R$
Death of I_R	$P(I_R \rightarrow I_R - 1)$	$:[(b + \alpha) I_R]/R$
Dispersal of S_G	$P(S_G \rightarrow S_G - 1)$	$:[m S_G(H_G + c_R H_R)/K_G]$

The events in Table 4.2 are incremented at random and the associated probabilities are updated following population density changes after each event. The time

between events is an exponentially distributed random variable, $T_{\text{event}} = -\ln(\sigma)/R$ where σ is a random number from the uniform distribution between 0 and 1 (Renshaw (1991)). The model is coded using Fortran 90 and individual simulations are undertaken using a Gillespie algorithm and provide information of the behaviour in a single realisation (Renshaw (1991)). Multiple realisations are generated to assess the average behaviour and variability (see Chapter 3, White et al. (2014, 2016b) for further details of the model set-up).

To simulate the replacement of red squirrels by greys on Anglesey the model was initialised with the red squirrel abundance and known distribution as shown in Figure 4.1 (at the end of the 25 year period) representing the conditions in 1966. Grey squirrels were introduced at the Britannia Bridge and model dispersal parameters that led to the (near) replacement of red squirrels and the expansion and increase in abundance of grey squirrels were fitted so that the abundance of grey squirrel was between 3000-4000 by 1998 (after 33 years in the model). Details of fitting the dispersal distance and dispersal parameter (m) to the observed squirrel populations are given in (see Chapter 3). Here it was found that the maximum dispersal distance of 2 km and the dispersal parameter of $m = 2b$ (which represents that an individual squirrel makes on average two long distance relocations in its lifetime) was required to enable grey squirrels to expand across Anglesey and replace most red squirrel populations in 33 years, which closely matched field observations. In this study we wish to adapt the model to represent the control and eradication of grey squirrels and the reintroduction and expansion of red squirrels as reported on Anglesey between 1998-2013.

Grey squirrel control and the reintroduction of red squirrels on Anglesey

In the 1990s, a conservation project was undertaken to conserve and increase the remaining red squirrel population on Anglesey, (Forum, 2009; Shuttleworth, 2003). From 1998 - 2002, the primary aim was to increase the red squirrel population on Anglesey by removing grey squirrels, mostly in the south of the island (Ogden et al., 2005). Following initial successes, the grey squirrel control effort on Anglesey (and the mainland adjacent to the Britannia Bridge) was expanded and intensified and was coupled with a reintroduction program of red squirrels from 2004 - 2013. The regions in which control was applied and the locations for red squirrel reintroductions are shown in the supplementary information, Figures 4.A.1-4.A.2 and data on the control effort and the number of grey squirrels caught is available in (Schuchert et al., 2014) and shown in Table 4.3.

Table 4.3: The control effort and number of grey squirrels caught on Anglesey and the mainland (adjacent to the Britannia Bridge) for the grey squirrel eradication programme reported in Schuchert et al. (2014). In 2013, 1 grey squirrel was dispatched prior to being caught.

Year	Anglesey		Mainland	
	Trapdays	Greys caught	Trapdays	Greys caught
1998	16923	1100	0	0
1999	14000	700	0	0
2000	17391	800	1380	0
2001	18571	520	1380	0
2002	35591	1128	1380	177
2003	30959	421	1042	156
2004	27546	419	668	38
2005	27758	587	0	0
2006	35039	165	0	0
2007	52414	237	276	36
2008	38300	146	2098	254
2009	33698	105	2126	160
2010	23392	49	4706	597
2011	6832	3	4550	425
2012	24105	22	4735	506
2013	16317	0 (1)	6305	508

We consider two control strategies in an attempt to match the data of (Schuchert et al., 2014). Control strategy 1 focuses control on suitable woodland sites (Shuttleworth, 2003), which we assume to be grid squares with potential density $K_G > 3$ in the model, within the specified control regions (Figure 4.A.3) for the entire control period 1998-2013. We divide the total trapdays (Table 4.3) by the number of suitable grid cells to provide the trap effort per grid cell per year. For each year between 1998-2013 we convert this to the trap effort per grid cell per day, T_i (T_A for Anglesey, T_M for the mainland) by assuming trapping occurs for 6 months between April and September (183 days). The maximum trap effort per grid cell per day occurred on the mainland in 2013: $T_{\max} = 3.14$. Control strategy 2 uses the same method as strategy 1 on the mainland and on Anglesey between 1998 - 2005. Between 2005-2013 the strategy on Anglesey is changed to focus on grid cells where grey squirrels remain. Here, control was applied in grid cells where grey squirrels were present and in a 2 km buffer around these grid cells at either a level to reflect the trap effort per day per grid cell or at T_{\max} , which ever is smaller. Any remaining

trapdays were distributed across cells in which $K_G > 3$ in the trappable region.

The inclusion of grey squirrel control introduces additional events (to those listed in Table 4.2). For example the probability of trapping and removing a susceptible grey squirrel is represented as follows

$$\text{Control of } S_G \quad P(S_G \rightarrow S_G - 1) \quad : [cT_i(S_G)] / R$$

where c reflects the rate of capture per trap effort per day. Similar terms are included for all squirrel classes but if a red squirrel is caught there is no change in density (to represent that it is released). To compare the model findings with the observed data we ran 20 realisations of model for 16 years (1998-2013) including trapping for different values of $c \in [2.0, 5.0]$ starting with initial conditions to reflect the grey squirrel density and distribution in 1998 (see Figure 4.A.4). Red squirrel reintroductions were included at the sites documented during 2004 - 2013 (Craig Shuttleworth, pers.comm., Figure 4.A.2). Extinction of grey squirrels on Anglesey occurred by 2013 (Halliwell et al., 2015) and therefore we required that grey squirrel extinction in the model occurred on Anglesey in greater than 50% of the realisations between 2011-2013 (and that it did not occur in greater than 50% of the realisations before 2011). In addition to this criteria we tested which control scenario and value of c gave the best fit to data in terms of minimising the following statistic

$$S = \sum_{i=1998}^{2010} \frac{(E_i - O_i)^2}{E_i} \quad (4.6)$$

where E_i is the number of greys caught in the model in year i and O_i is the actual number caught. S is averaged over all realisations.

In Figure 4.2 we present the best fits to data for the two control scenarios (with further results shown in Figures 4.A.5-4.A.8). These indicate that strategy 2 provides the best fit to the observed data (and so provides a best estimate of $c = 3.5$). Here, all key woodland sites are initially targeted and later control is focussed where grey squirrels are still present. We now use the model to examine whether a more efficient control strategy could have been used to eradicate grey squirrels from Anglesey and to develop strategies to maintain and protect the established red squirrels on Anglesey from future invasion.

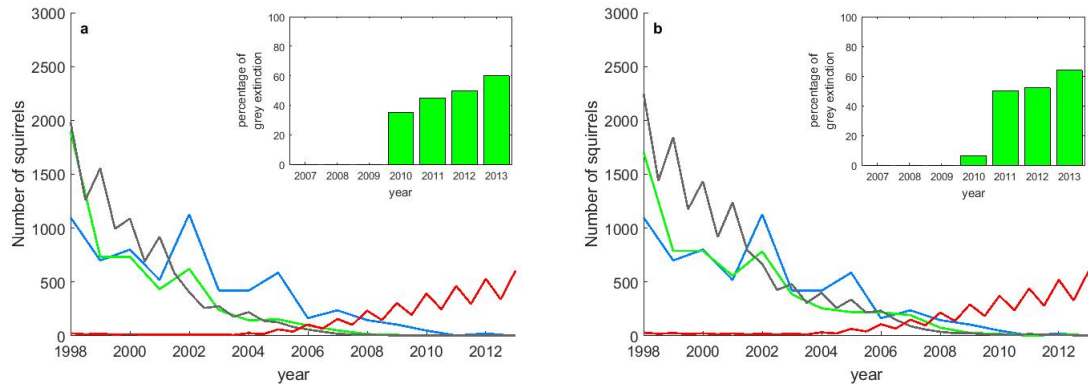


Figure 4.2: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under (a) control strategy 1 with $c=4.4$ and (b) control strategy 2 with $c=3.5$. The blue line shows the actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, both scenarios satisfy the criteria that 50% of realisations should show grey extinction between 2011-2013 (but not prior to this time) and the best fit statistic is $S=6867$ for scenario 1 and $S=2072$ for scenario 2.

4.4 Results

4.4.1 Alternative eradication strategies

Using the same number of trapdays as in the 1998-2013 eradication campaign (Table 4.3), we used the model to test different control strategies to determine if the grey squirrels on Anglesey could have been eradicated more quickly. The general method that was tested was to apply grey squirrel control in the best habitat first and then increase the region over which control was applied in response to trapping data. Three specific approaches are outlined in Table 4.4. In particular in trapping approach A, trapping occurs in the best 10% of habitat until the number of grey squirrels caught dropped below 25% of the initial trapping value, then trapping is applied to the best 20% of habitat until the number caught drops below 25% and then trapping is applied in regions where greys are still present (and a buffer around these regions). Figure 4.3 shows the results for the different approaches and indicates that trapping approach B would lead to the fastest eradication of grey squirrels on Anglesey. (Note: we also tested these trapping approaches when the change between stages was triggered if the number of greys caught fell below 50%

and 10% of the initial number caught (see Figure 4.A.9). The value of 25% shown in Figure 4.3 gave the best results). These results suggest that grey squirrels could have been eradicated from Anglesey by 2010 using the same trap effort per year as in the actual eradication programme (in which eradication occurred by 2013).

Table 4.4: The details of three alternative trapping approaches that could have been used to remove grey squirrels from Anglesey. Stage 1 traps in the most suitable habitat first - determined as the specified percentage of habitat with the highest potential density. When the number of grey squirrels trapped drops below 25% of the initial number caught, the trapping approach changes to stage 2 in which trapping is applied in the specified percentage of habitat with the highest potential density. When the number of grey squirrels caught in stage 2 drops below 25% of the initial number caught in this stage, the approach changes to stage 3. In stage 3 trapping is applied to all grid cells in which grey squirrels are present and habitable grids cells within a 2 km buffer around occupied grid cells. In all trapping approaches grey control is applied on the mainland in the cells indicated in Figure 4.A.3 at the levels reported in Table 4.3.

Trapping approach	Stage 1 (% of habitat trapped)	Stage 2 (% of habitat trapped)	Stage 3
A	10	20	All $H_G > 0$ grid cells plus 2 km buffer
B	20	40	All $H_G > 0$ grid cells plus 2 km buffer
C	10	40	All $H_G > 0$ grid cells plus 2 km buffer

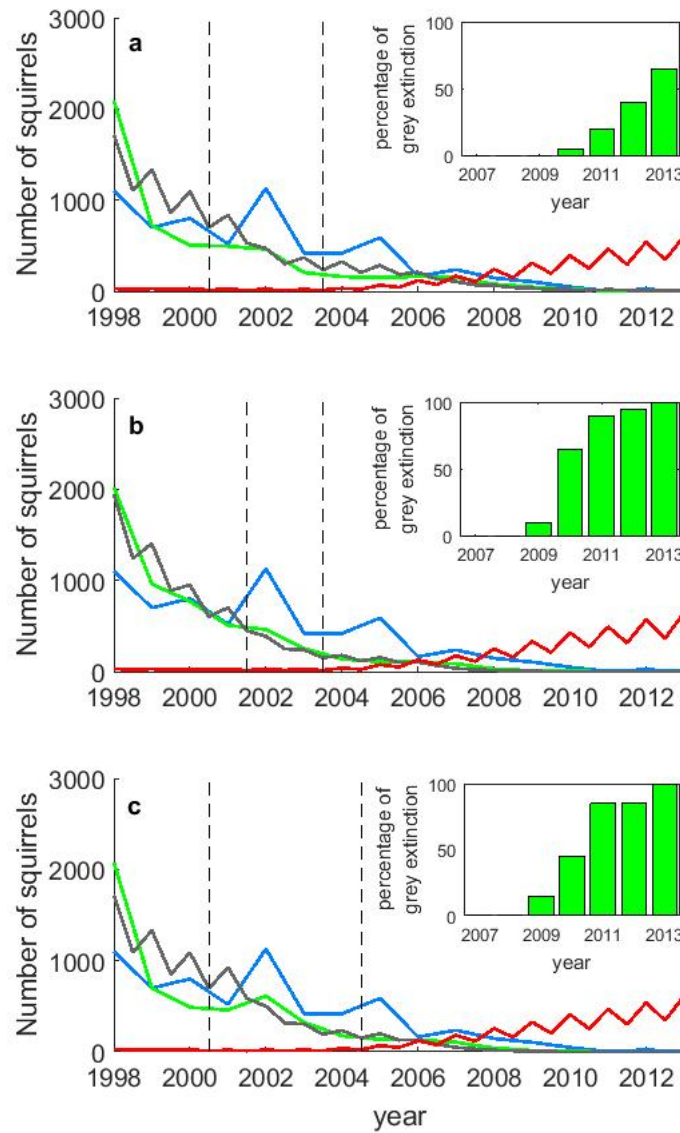


Figure 4.3: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under (a) trapping approach A, (b) trapping approach B and (c) trapping approach C (see Table 4.4). The blue line shows the actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year.

4.4.2 Strategies to protect red squirrels on Anglesey

To highlight the importance of ongoing control of grey squirrels for the protection of red squirrels, we undertook model simulations in which grey squirrel control was stopped from 2014 onwards (Figure 4.4). The model predicts that grey squirrels will disperse from the mainland to Anglesey and that the replacement of red squirrels by greys would occur within approximately 35 years (this is similar to the observed red replacement on Anglesey between 1966-1998). This highlights the importance of continued grey squirrel control to protect the red squirrel populations on Anglesey. The model was therefore used to develop resource efficient grey squirrel control strategies that could be included in current and future red squirrel conservation policy.

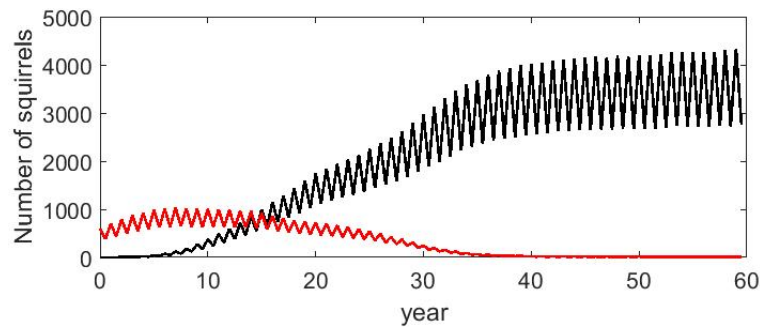


Figure 4.4: Average of 20 model realisations from 2014 - 2074 showing grey and red squirrel abundance on Anglesey if grey squirrel control is ceased on Anglesey and the mainland in 2014.

To estimate the trap effort required to maintain red squirrel populations on Anglesey we considered a range of strategies of control on the mainland, adjacent to the Britannia Bridge, and on Anglesey. We assume control on the mainland occurs for 6 months each year at a percentage of the maximum control effort (T_{max}). Furthermore, we assume control occurs on Anglesey in response to sightings of grey squirrels. In the model we approximate this with control occurring for one month in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present (again with an effort that is a percentage of T_{max}). The different combinations are presented in Table 4.5 (with results for the different control level combinations shown in Figures 4.A.10-4.A.17). Control methods 1 and 2, which have no or limited control on the mainland, but high intensity control on Anglesey in response to grey detection, do succeed in protecting red populations on Anglesey (Figures 4.A.10-4.A.11). However, the dispersal of grey squirrels from the mainland means there is a continual presence of grey squirrels on Anglesey, and therefore a need for a high level of trapping in response to grey squirrel detection. Since grey squirrel

detection on the ground will rely on reporting from the general public, a control method that limits the grey squirrel presence on Anglesey would be more desirable. Only two combinations prevent grey squirrels from establishing on Anglesey and of these the method with the lowest trapping effort suggests that the mainland should be trapped at 50% of T_{max} and the response to sighting of grey squirrel on Anglesey should be at T_{max} . The population and epidemiological dynamics and trap effort in the model for this scenario is shown in Figure 4.5. Red squirrel densities on Anglesey are conserved and grey squirrels are detected on Anglesey at sporadic intervals and low levels. The number of trapdays per year to achieve this level of control required there to be a continual effort of 3153 trapdays per year on the mainland and then responsive control that ranges from zero to 3726 trapdays per year on Anglesey. Control scenarios in which trapping on Anglesey occurred at less than T_{max} failed to prevent grey squirrels from establishing on Anglesey and in some scenarios led to a significant decline in red squirrel abundance (Figures 4.A.14-4.A.17). As grey squirrels do disperse to Anglesey, there is a risk of squirrelpox being spread to red squirrels. The model suggests that squirrelpox outbreaks in red squirrels will only affect a small number of red squirrels (Figure 4.5). The spread of squirrelpox throughout the established red squirrel population on Anglesey did not occur in model simulations.

Table 4.5: Control strategies to protect the red squirrel stronghold on Anglesey after eradication of grey squirrels. The trap effort per grid cells per day as a percentage of T_{max} on Anglesey (T_A) is shown in column 2 and the trap effort per grid cell per day as a percentage of T_{max} on the mainland adjacent to the Britannia Bridge (T_M) is shown in column 3. If realisations have occurred in which > 50 grey squirrels were present during the year on Anglesey, the control method is not adequate (column 4, marked with “Yes”).

Continual control method	T_A (% of T_{max})	T_M (% of T_{max})	> 50 greys on Anglesey	Average trapdays
1	100	0	Yes	2484
2	100	10	Yes	2224
3	100	50	No	3395
4	100	100	No	6420
5	50	50	Yes	4045
6	50	100	Yes	6549
7	10	50	Yes	4193
8	10	100	Yes	7102

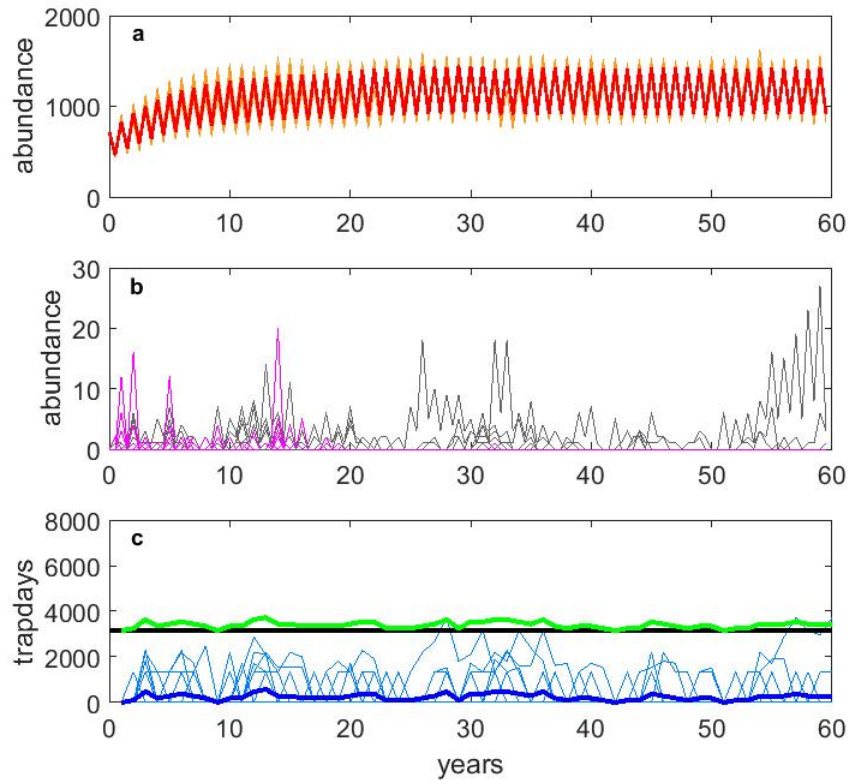


Figure 4.5: Model results using control method 3 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue - this shows that, in general, little control is required on Anglesey), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 50% of T_{max} and control occurs at T_{max} for one month in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

4.5 Discussion

We have developed a mathematical model encapsulating the red squirrel, grey squirrel and squirrelpox system that can represent the real-life trapping and removal of grey squirrels in landscapes that are the subject of ongoing management intervention. The model provided a good representation of the observed removal of grey squirrels from Anglesey between 1998-2013. The model also allowed alternative control strategies to be considered that may have better utilised the limited finances available to implement trapping effort on Anglesey. In particular, a control strategy that initially focussed on the best grey squirrel habitat, to reduce the impact of source populations, before switching to more widespread grey control was shown to

eradicate grey squirrels from Anglesey by 2010, three years earlier than in the field. This highlights the potential of mathematical models in the design of eradication and control programmes.

The mathematical model was also used to determine the effort required to protect the red squirrel population on Anglesey from future grey squirrel invasion. The model provided quantitative predications that recommended a continual trapping effort in mainland sites adjacent to the Britannia Bridge to minimise grey dispersal to Anglesey, and high intensity trapping in response to observations of grey squirrels that do reach Anglesey. The model suggest that this strategy requires on average (mean) 3395 trap days per year, with a range of 3153 - 6878, dependent on whether trapping was required on Anglesey. This mean shows that in general, the squirrel trapping required on Anglesey is low (as the large range does not increase the mean much) and therefore effort is largely only required on the mainland (3153 trap days per year). This equates to the effort comfortably encompassed by one full time grey squirrel trapping operative. This predicted control effort was shown to maintain a stable population of approximately 1000 red squirrels on Anglesey. It is worth noting that if grey control was not continued then grey re-invasion and complete replacement of red squirrels would re-occur within 35 years. These projections can be used to support regional policy and funding decisions to efficiently protect red squirrels on Anglesey (Shuttleworth et al., 2015c).

The mathematical model developed in this study can be used to shape policy and design conservation strategy in other regions in which grey squirrel invasion is a threat to red squirrels. For instance the current conservation strategy in the UK is to protect red squirrels by using grey squirrel control in and around designated red squirrel strongholds/priority regions (RSNE, 2016) and along a containment region that spans from east to west Scotland in the Scottish Highlands. By extracting habitat specific information from digital landcover data for these regions, the model could forecast the likelihoods of grey squirrel establishment and determine the control effort (in terms of trapdays) required to protect red squirrel populations. This would provide the key information of where and how much control should be applied and allow red squirrel conservation organisations to better utilise current resources and to plan future resource requirements. Model investigations, in collaboration with Saving Scotland's Red Squirrels (Saving Scotland's Red Squirrels, 2016), to determine the distribution and level of control required to protect red squirrels in Scotland are ongoing and will form the basis of future studies (Gurnell et al., 2015; Scottish Squirrel Group, 2015). In particular, advice on levels of control to prevent further range expansion of grey squirrels in the Highlands is critical to protect the current widespread and abundant red squirrel populations. The likelihood of recovery of grey squirrel populations after control programmes is also considered (Lawton

and Rochford, 2007).

The trapping effort reported to eradicate grey squirrels from Anglesey is a valuable long term and “real-world” data set that highlights the challenges of landscape control (see Parrott et al. (2009); Schuchert et al. (2014); Shuttleworth et al. (2015a)) for retrospective critical reviews). We note that other mammalian eradication studies have highlighted the potential for trappers to try to prolong a project by trapping at a lower rate than those reported (Gosling and Baker, 1989). Such issues may arise when there is a lack of incentives to complete the work, with a fear of unemployment if the species is eradicated (Gosling and Baker, 1989). To assess the importance of trapping efficiency, we ran the best fit model for Anglesey (Figure 4.2b) using (a) 80% and (b) 120% of the reported trap effort of Table 4.3. Scenario (a) represents when trappers reported a greater number of hours than were actually worked and results indicate that grey squirrels would not be eradicated with this level of control (Figure 4.6a). Scenario (b) represents when trappers reported the correct hours but were not working at full efficiency. Here, if the higher level of control had been applied, grey squirrel extinction could have occurred around 2009-2010 (Figure 4.6b). This highlights the need for correct incentives and close management of staff in conservation projects. Management oversight during eradication did indeed find isolated examples of a contractor failing to distribute traps thoroughly across a woodland (Shuttleworth, personal observation). Parallels can be drawn with the eradication of the coypu in the UK (Gosling and Baker, 1989). Here, a bonus scheme that incentivised early eradication of coypus was employed and this is considered to have played a major role in the successful eradication (Gosling and Baker, 1989).

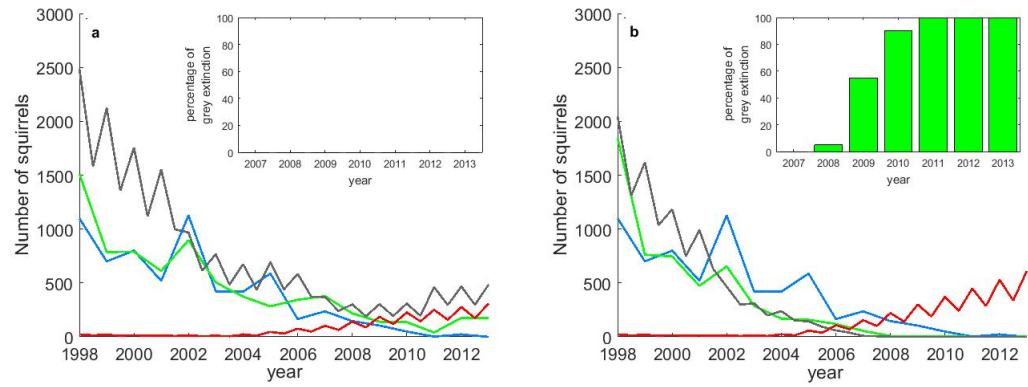


Figure 4.6: Increased and decreased trapping competence with (a) 80% of trap effort and (b) 120% of trap effort. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year.

The model also allows for an assessment of the impact of squirrelpox on the effort to conserve red squirrels on Anglesey. While future grey control could limit the dispersal of grey squirrels to Anglesey, it could not prevent occasional incursions (as evidenced by three greys removed from the island in autumn 2015 (Shuttleworth, 2016)). The model predicts that the dispersal of infected grey squirrels could lead to squirrelpox transmission to red squirrels. However, within the established red squirrels, squirrelpox outbreaks are localised and the infection fades out and does not spread widely throughout the population. Squirrelpox, is therefore predicted to have a minor effect on the total red population abundance on Anglesey. This confirms previous model findings (Chapter 3, Macpherson et al. (2016a); White et al. (2016a,b) and evidence from the field where squirrelpox outbreaks in red squirrel populations in protected stronghold regions are short-lived, with red squirrel abundance returning to pre-infection levels following disease fade-out (Chantrey et al., 2014; White and Lurz, 2014). The evidence therefore suggests that grey squirrel control in and around vulnerable red squirrel populations should be the primary strategy for red squirrel conservation, rather than focussing on preventing the spread of squirrelpox. Localised outbreaks of squirrelpox in protected red squirrel populations may occur as an unavoidable consequence of red populations being adjacent to squirrelpox carrying greys. Provided greys are prevented from establishing in protected red squirrel strongholds then red density can, over time, return to pre-infection levels following an outbreak (White et al., 2014, 2016a).

Well-developed conservation strategies are required to protect native species from

the threat of invasion. In this study we have shown how mathematical modelling can play a key role in policy and planning to eradicate or manage invasive species. The model has been applied to the key case study system of the invasion of grey squirrels in the UK. The approach is based on combining well understood mathematical modelling frameworks with spatial information on habitat distribution, structure and actual levels of control. The approach could therefore be applied to a wide range of systems in which invasive species pose a threat to native species and ecosystems.

4.6 Acknowledgements

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4.7 Additional work on this topic - “Painting the Town Red”

To maintain the red squirrel population on Anglesey and further increase red squirrel numbers in north Wales, the project “Painting the Town Red” was also proposed by the Red Squirrel Survival Trust (RSST). The project proposed the eradication of the grey squirrel populations in and around Bangor (see Figure 4.7). This was considered a viable strategy as the Snowdonian mountains which surround Bangor provide a natural boundary which limit much of the dispersal of grey squirrels into the area. The key dispersal routes are therefore between the mountains and the coast to the north east and the south west of Bangor. The motivation for this proposed strategy is that removing the grey squirrels from the Bangor area would allow red squirrels from Anglesey to disperse and establish on the mainland. This would further increase red squirrel densities and significantly reduce the chance of any grey squirrels getting to Anglesey, thus securing this stronghold population. In this section we will use the trapping rates obtained earlier in this chapter to predict the cost in trapdays of clearing and maintaining a grey squirrel free mainland area and compare it to the effort required to maintain a red squirrel stronghold on Anglesey only.

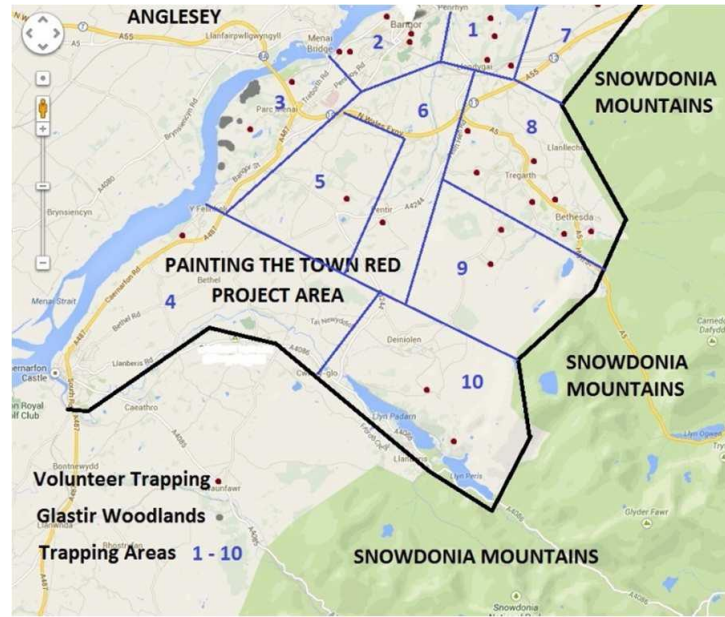


Figure 4.7: The proposed regions for grey squirrel removal in the Painting the Town Red project as proposed by RSST (Shuttleworth, pers. comm.).

Using the potential densities of red and grey squirrels at a 1 km x 1 km patch level as obtained in Section 4.3.1, we mapped the region approximating that shown in Figure 4.7 (region 1, Figure 4.8a), along with a larger region in which a smaller pinch point between the coast and the Snowdonian mountains forms the north east border of the region and the south western border is further south and extends to the west coast (region 2, Figure 4.8b). The natural barrier of the mountain range (where $K_G = 0$) can be seen. The dispersal corridor on the north east coast is narrow so it is expected that only a small number of grid cells would need continual grey squirrel control once the mainland region is cleared. However, the south west of the mainland study area has a larger area of suitable squirrel habitat between the mountains and coast so it is likely that more control effort would be required to prevent grey squirrel spread from the south.

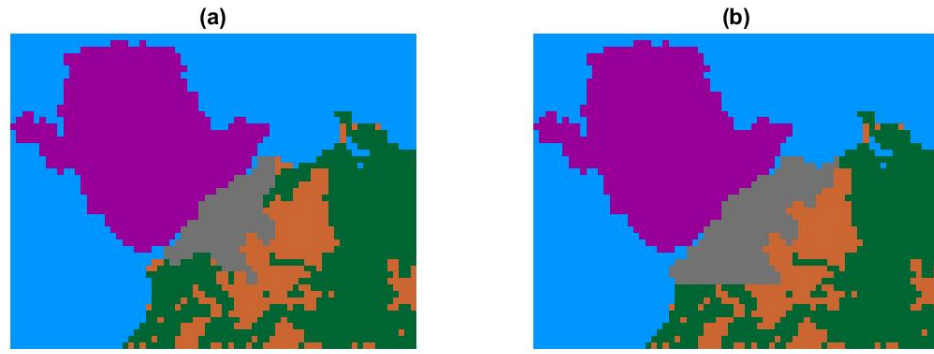


Figure 4.8: Map of study area proposed for clearing of grey squirrels with (a) region 1 (as proposed by RSST) and (b) region 2 (larger region with smaller habitable pinch points at the boundaries of the region) coloured grey. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown.

4.7.1 Mainland control method 1

The first method proposed to eradicate grey squirrels from these regions uses the strategy found to be most efficient when modelling the Anglesey eradication process (trapping approach B, see Table 4.4). Initially, control occurs in the best 20% of habitat during the six month trapping season until the number caught drops below 25% of the initial trapping value, then trapping is applied to the best 40% of habitat until the number caught drops below 25% and then trapping is applied in regions where greys are still present (and a buffer around these regions). Trapping is implemented at the maximum rate used previously ($T_{max} = 3.14$). Meanwhile, for the month of October, trapping occurs at T_{max} for one month at any sites on Anglesey in which grey squirrels have been sighted at the start of October ($H_G > 0$) and in a 2 km buffer (providing $K_G > 0$) around these grid cells. The initial conditions were taken as the squirrel population densities/locations in a typical model realisation in 2013 (in which grey squirrels were eradicated from Anglesey and squirrelpox is present on the mainland). The total grey population in the study area decreases significantly due to control, so the chance of squirrelpox dying out in the study area is high. Therefore, to incorporate the chance of squirrelpox dispersing in from outside the study area, one infected grey squirrel is introduced near the south west boundary and one by the far eastern boundary of the mainland control region each year. Simulations using this control strategy (20 realisations run for 60 model years) found that the switch between stage 1 and stage 2 (trapping in the best 20% to trapping in the best 40% of habitat) occurred after approximately 4 years but that the switch to stage 3 (invoked when number of greys caught in the best 40% of

habitat drops below 25% of the initial number caught) rarely occurred. Therefore grey squirrel eradication rarely occurred in the 60 year model time scale.

As the initial control strategy was unsuccessful in eradicating grey squirrels from the mainland we propose a new strategy (mainland control method 1) in which the time that the switch to stage 2 and stage 3 occur is fixed to be after 4 years and after 8 years respectively. Eradication of grey squirrels now occurred in both regions but on average, a higher number of trapdays are required in the long term in region 1 due to the larger pinch points between natural boundaries at the edges of the region (despite region 1 being smaller in area than region 2, see Figure 4.9-4.10).

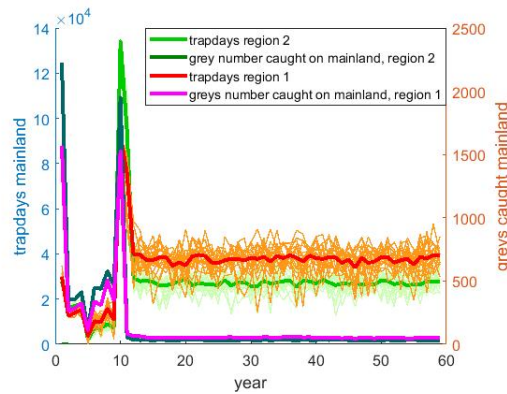


Figure 4.9: The number of trapdays and number of grey squirrels caught using mainland control method 1. The average number of trapdays of 20 realisations over 60 years are shown in bold red/green (left axis) and the average number of grey squirrels caught on the mainland are shown in bold purple/dark green (right axis) for regions 1 and 2 respectively. The number of trapdays for each realisation are shown in orange/green for regions 1 and 2 respectively. $T_{max} = 3.14$ is applied during the trapping period each year.

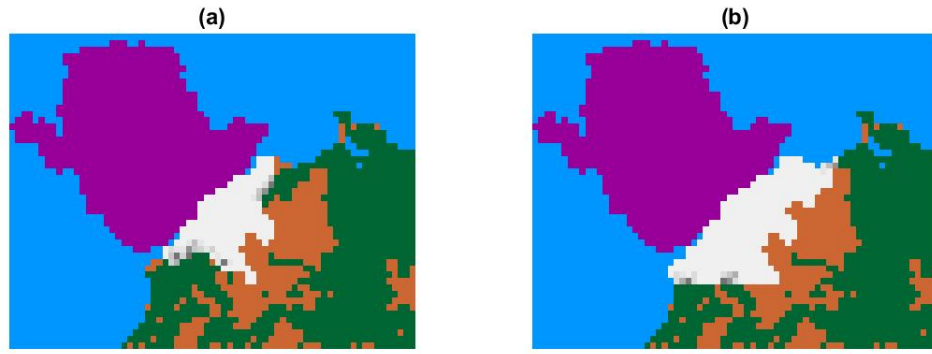


Figure 4.10: Map showing the percentage of realisations in which trapping still occurred after 60 years for (a) region 1 and (b) region 2, as shades of grey (dark grey is 100% of realisations and white is 0%) under mainland control method 1. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown. $T_{max} = 3.14$ is applied in appropriate cells during the trapping period each year.

To assess whether grey control could be achieved for a reduced number of trap-days, we consider the mainland control method 1 strategy but with the level of control in each grid cell reduced to 50% and 10% of T_{max} , see Figure 4.11. Using an effort of only 10% of T_{max} does not keep the designated mainland area clear of grey squirrels (trapping is occurring throughout most of both regions after 60 years, see Figure 4.12) and therefore, grey squirrels can reach Anglesey and so control is required there too (Figure 4.14). With control at 50% of T_{max} , the regions remain clear of grey squirrels except at the north east and south west pinch points (Figure 4.13). Thus trapping with 50% of T_{max} on the mainland can adequately remove grey squirrels. As previously, region 2 is more economically viable in the long-term, requiring an average 14601 trapdays per year on the mainland to control grey squirrels (and none on Anglesey, see Figure 4.15). Anglesey remains grey squirrel and squirrelpox free and the cleared mainland region 2 can support 976 red squirrels.

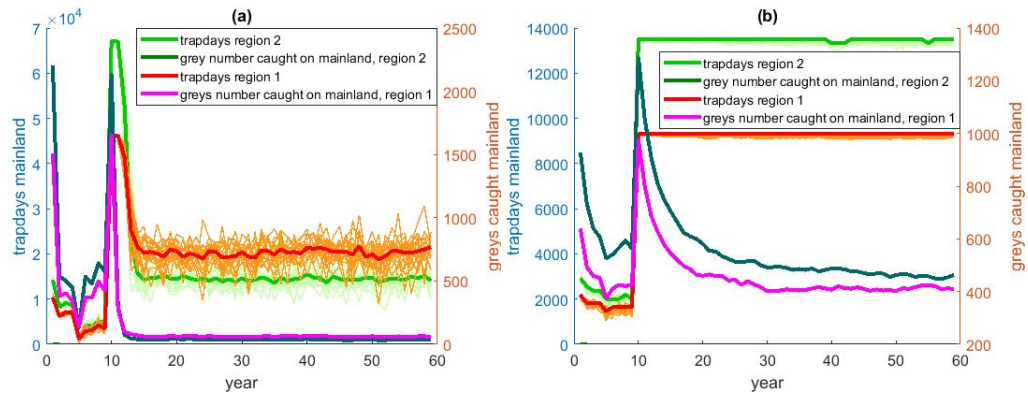


Figure 4.11: The number of trapdays and number of grey squirrels caught using mainland control method 1. The average number of trapdays of 20 realisations over 60 years are shown in bold red/green (left axis) and the average number of grey squirrels caught on the mainland are shown in bold purple/dark green (right axis) for regions 1 and 2 respectively. The number of trapdays for each realisation are shown in orange/green for regions 1 and 2 respectively. (a) 50% of T_{max} (1.57) and (b) 10% of T_{max} (0.31) are applied during the trapping period each year.

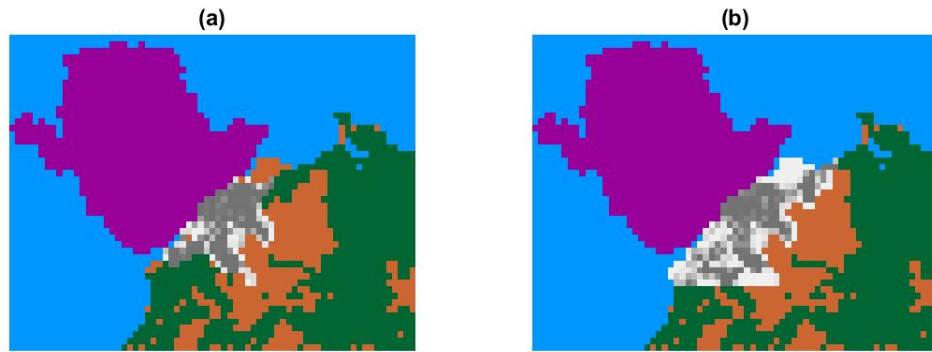


Figure 4.12: Map showing the percentage of realisations in which trapping still occurred after 60 years for (a) region 1 and (b) region 2, as shades of grey (dark grey is 100% of realisations and white is 0%) under mainland control method 1. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown. 10% of T_{max} (0.31) is applied in the appropriate cells during the trapping period each year.

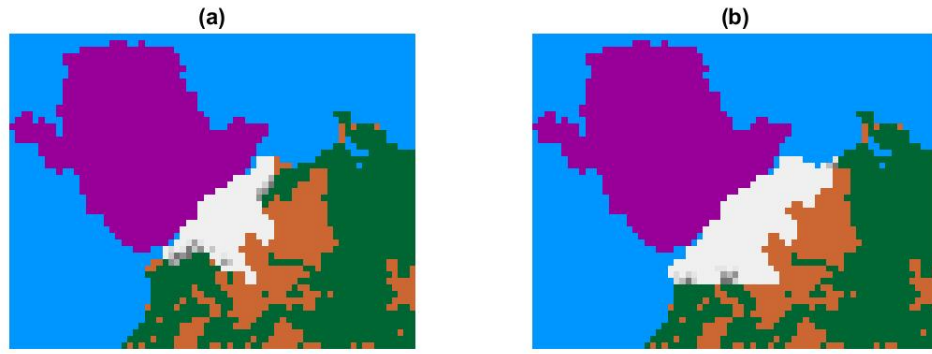


Figure 4.13: Map showing the percentage of realisations in which trapping still occurred after 60 years for (a) region 1 and (b) region 2, as shades of grey (dark grey is 100% of realisations and white is 0%) under the mainland control method 1. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown. 50% of T_{max} (1.57) is applied in appropriate cells during the trapping period each year.

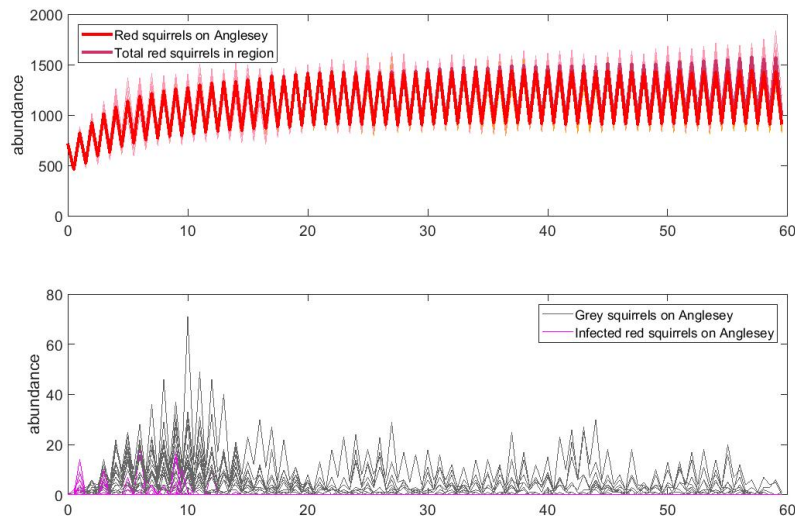


Figure 4.14: Squirrel densities on Anglesey with 10% of T_{max} (0.31) being applied using mainland control method 1 with the model set up as in Figure 4.11b. Trapping also occurs on Anglesey at T_{max} (3.14) during October in grid cells with $H_G > 0$ and within a 2 km surrounding buffer providing $K_G > 0$.

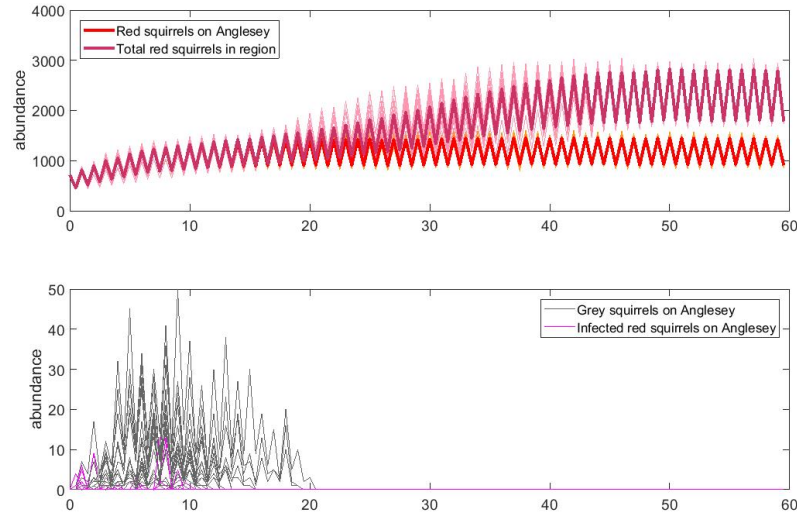


Figure 4.15: Squirrel densities on Anglesey with 50% of T_{max} (1.57) being applied using mainland control method 1 with the model set up as in Figure 4.11a. Trapping also occurs on Anglesey at T_{max} (3.14) during October in grid cells with $H_G > 0$ and within a 2 km surrounding buffer providing $K_G > 0$.

4.7.2 Mainland control method 2

We also propose an alternative grey squirrel control strategy (mainland control method 2) to eradicate grey squirrels from regions 1 and 2. This method initially applies control in all habitable grid cells ($K_G > 0$) and when the number of grey squirrels caught drops below 25% of the initial number caught it switches to controlling in all grid cells with $H_G > 0$ at the start of the trapping season and in a surrounding 2 km buffer (when $K_G > 0$) (the same as control stage 3 in previous strategy). Taking trap effort to be at its maximum every year (T_{max}), 20 realisations were run with the same initial conditions as for mainland control method 1. Region 1 requires on average 92282 trapdays to initially clear the region (stage 1) with on average 37257 trapdays per year required subsequently (stage 2) to stop re-invasion (Figure 4.16a). Meanwhile region 2 requires initially on average 134124 trapdays, but subsequently stage 2 requires on average 26928 trapdays per year to stop grey re-invasion (Figure 4.16b).

The trap effort on the mainland was then applied at 50% and 10% of T_{max} . As with mainland control method 1, 50% of T_{max} is adequate to eradicate grey squirrels from both regions 1 and 2 (Figure 4.17a), while 10% of T_{max} did not eradicate grey squirrels (Figure 4.17b). Maps showing where trapping occurs after 60 years also highlight this, see Figures 4.18 - 4.19. Again, region 2 requires a higher initial number of trapdays, but once the area has been cleared of grey squirrels, a lower

number of trapdays are required to keep the region free of grey squirrels.

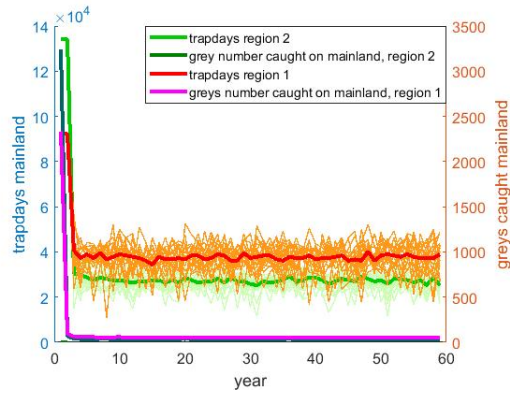


Figure 4.16: Trapdays used on the mainland compared with the number of grey squirrels caught over time in regions 1 and 2 using mainland control method 2. The average number of trapdays of 20 realisations over 60 years are shown in bold red/green (left axis) and the average number of grey squirrels caught on the mainland are shown in bold purple/dark green (right axis) for regions 1 and 2 respectively. The number of trapdays for each realisation are shown in orange/green for regions 1 and 2 respectively. $T_{max} = 3.14$ is applied in appropriate cells during the trapping period each year.

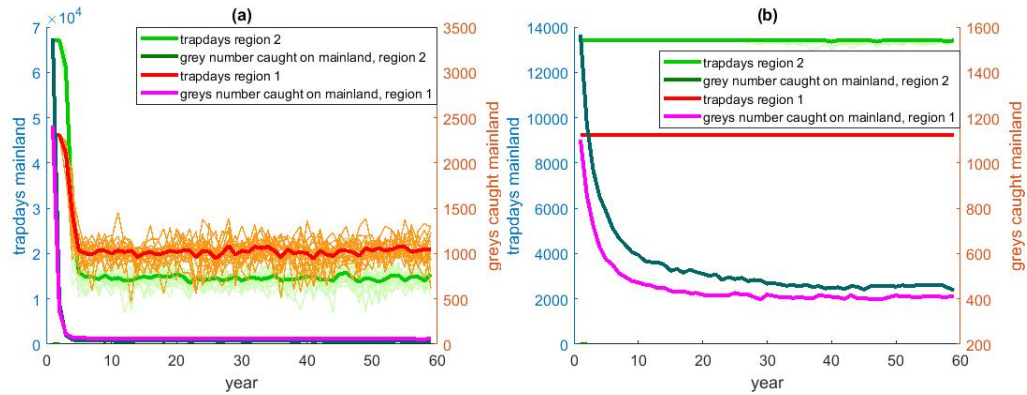


Figure 4.17: Trapdays used on the mainland compared with the number of grey squirrels caught over time in regions 1 and 2 using mainland control method 2. The average number of trapdays of 20 realisations over 60 years are shown in bold red/green (left axis) and the average number of grey squirrels caught on the mainland are shown in bold purple/dark green (right axis) for regions 1 and 2 respectively. The number of trapdays for each realisation are shown in orange/green for regions 1 and 2 respectively. (a) 50% of T_{max} (1.57) and (b) 10% of T_{max} (0.31) are applied in appropriate cells during the trapping period each year.

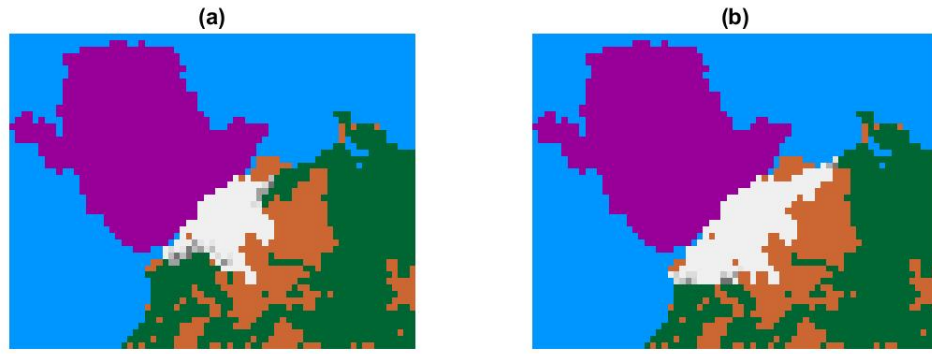


Figure 4.18: Map showing the percentage of realisations in which trapping still occurred after 60 years for (a) region 1 and (b) region 2, as shades of grey (dark grey is 100% of realisations and white is 0%) under mainland control method 2. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown. 50% of T_{max} (1.57) is applied in appropriate cells during the trapping period each year.

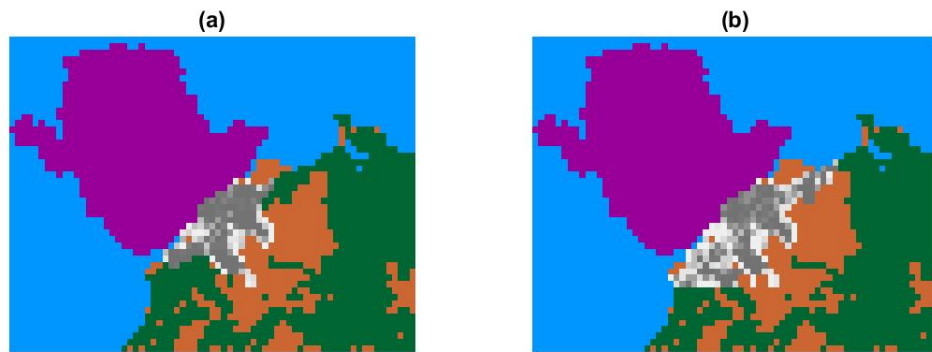


Figure 4.19: Map showing the percentage of realisations in which trapping still occurred after 60 years for (a) region 1 and (b) region 2, as shades of grey (dark grey is 100% of realisations and white is 0%) under mainland control method 2. Anglesey is shown in purple, cells that are habitable for grey squirrels ($K_G > 0$) are shown in green and cells that are uninhabitable ($K_G = 0$) are shown in brown. 10% of T_{max} (0.31) is applied in appropriate cells during the trapping period each year.

Comparing mainland control methods 1 and 2, both require a high level of trapping initially and control method 1 also requires a high level of trapping after 8 years. Both methods can remove grey squirrels from the control area and only require trapping at the north east and south west pinch-points in the long-term. Mainland control method 2 over region 2 requires the least control out of these methods with a predicted long-term effort of 14454 trapdays per year. This compares to an average long-term effort of 3395 trapdays required to maintain Anglesey

as a red squirrel stronghold. Therefore if resources are restricted, control on Anglesey alone using trapping approach B (Table 4.4) would be less resource intensive and may offer a long-term option for maintaining a viable population of red squirrels on Anglesey.

4.A Supplementary information: Mathematical models of invasive species management: Grey squirrel control on Anglesey

The following figures are referred to in this order in the main chapter.

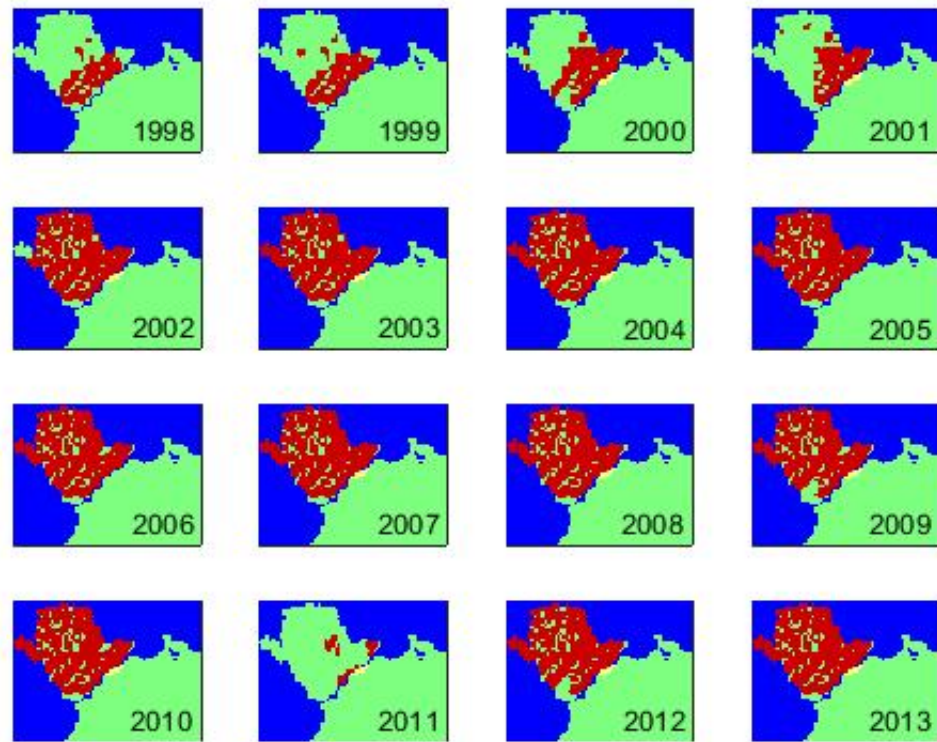


Figure 4.A.1: Maps showing the trapping regions used in the grey squirrel eradication programme between 1998-2013 for Anglesey (red) and the mainland (yellow) in which $K_G > 0$. Regions in which no trapping occurred or which did not contain suitable squirrel habitat are shown in green.

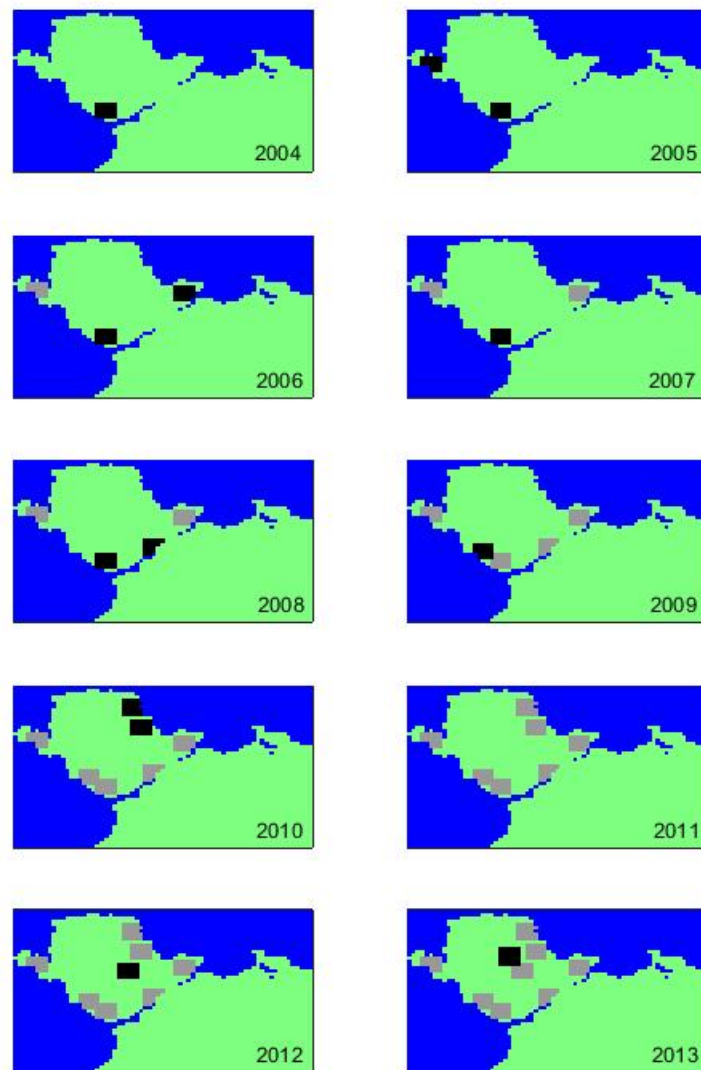


Figure 4.A.2: Maps showing the location of red squirrel reintroductions on Anglesey each year (black) and in previous years (mid grey) for 2004-2013.

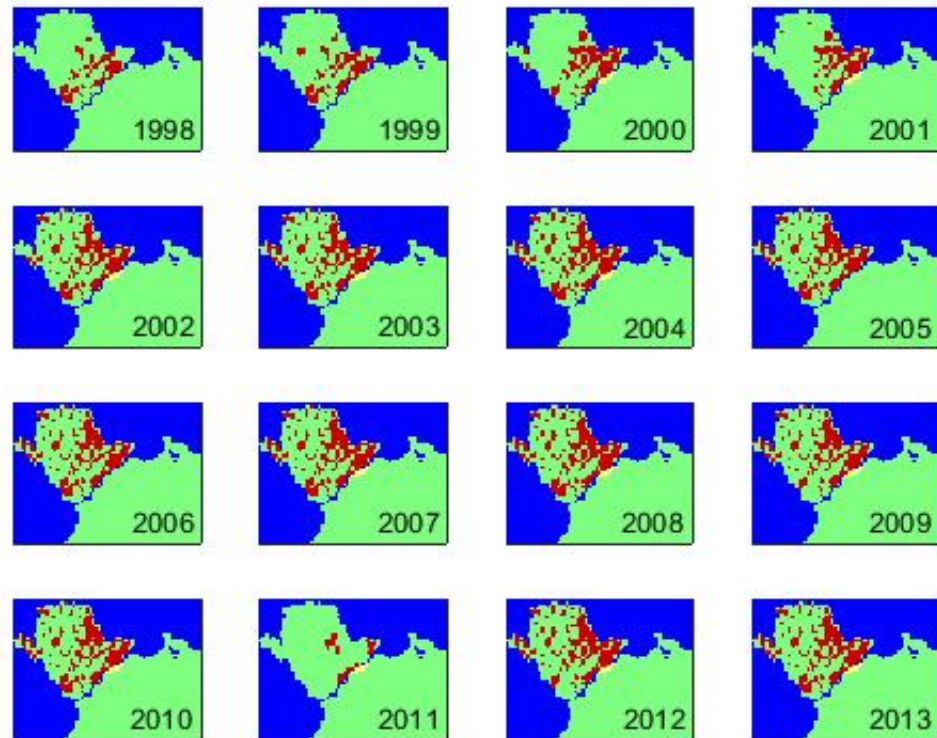


Figure 4.A.3: Maps showing the trapping regions used in the grey squirrel eradication programme between 1998-2013 for Anglesey (red) and the mainland (yellow) in which $K_G > 3$. Regions in which no trapping occurred or in which $K_G \leq 3$ are shown in green. By focusing on the better quality habitat ($K_G > 3$), it provides a better representation of where trapping would have occurred in the grey squirrel eradication programme.

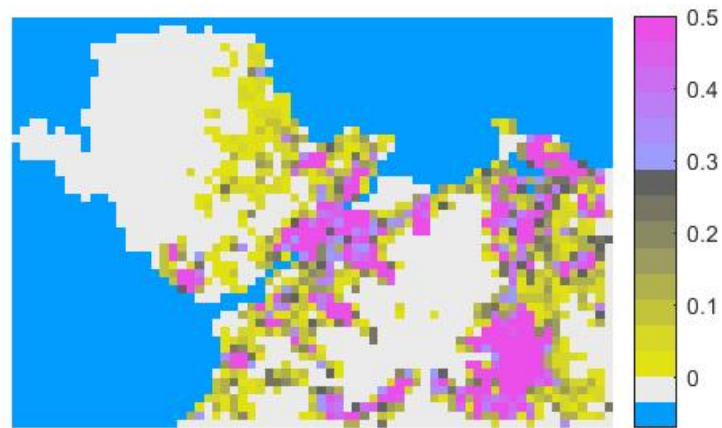


Figure 4.A.4: A map of the density (/ha) of grey squirrels on Anglesey and the mainland in 1998 before the onset of the grey squirrel control. (The colour bar indicates squirrel density per hectare which is determined by dividing the number of squirrels in each 1 km by 1 km cell by 100).

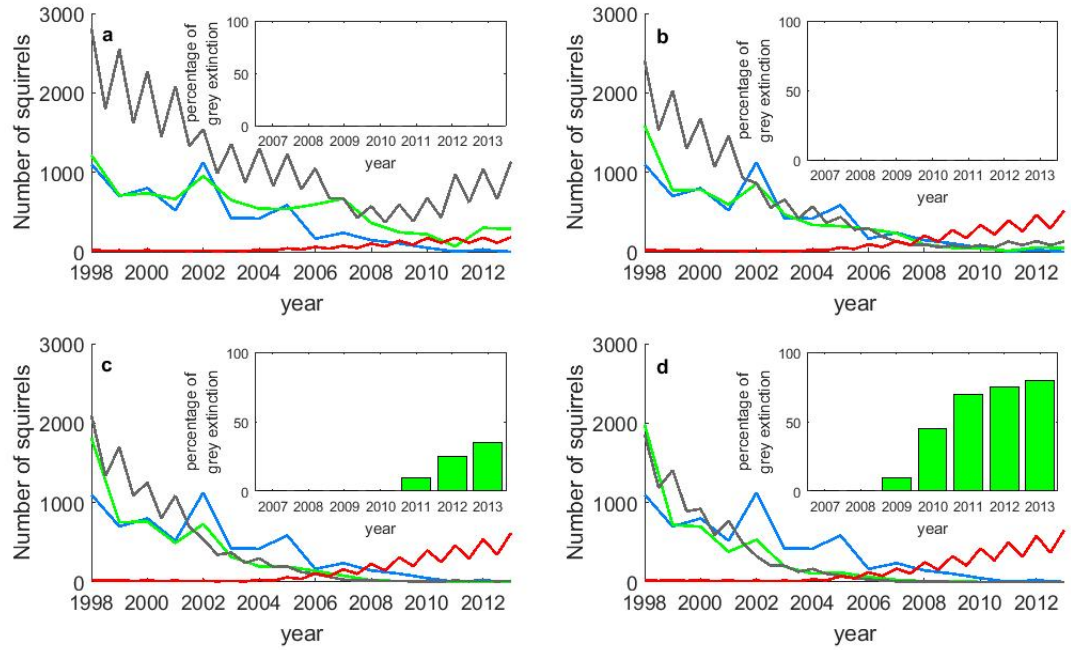


Figure 4.A.5: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under control strategy 1 with (a) $c=2.0$, (b) $c=3.0$, (c) $c=4.0$ and (d) $c=5.0$. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, only $c=5.0$ satisfy the criteria that 50% of realisations should show grey squirrel extinction between 2011-2013 (but not prior to this time) with the best fit statistic of $S=17668$.

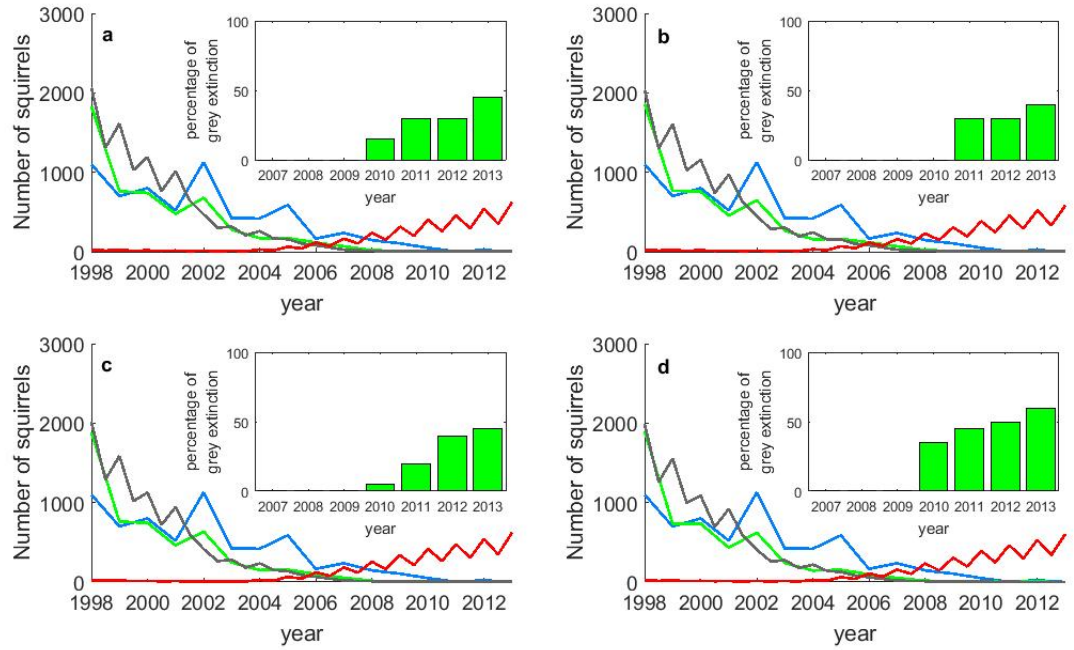


Figure 4.A.6: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under control strategy 1 with (a) $c=4.3$, (b) $c=4.4$, (c) $c=4.5$ and (d) $c=4.6$. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, $c=4.4$, $c=4.5$ and $c=4.6$ satisfy the criteria that 50% of realisations should show grey squirrel extinction between 2011-2013 (but not prior to this time) with the best fit statistics of $S=6867$, 9039 and 9649 respectively.

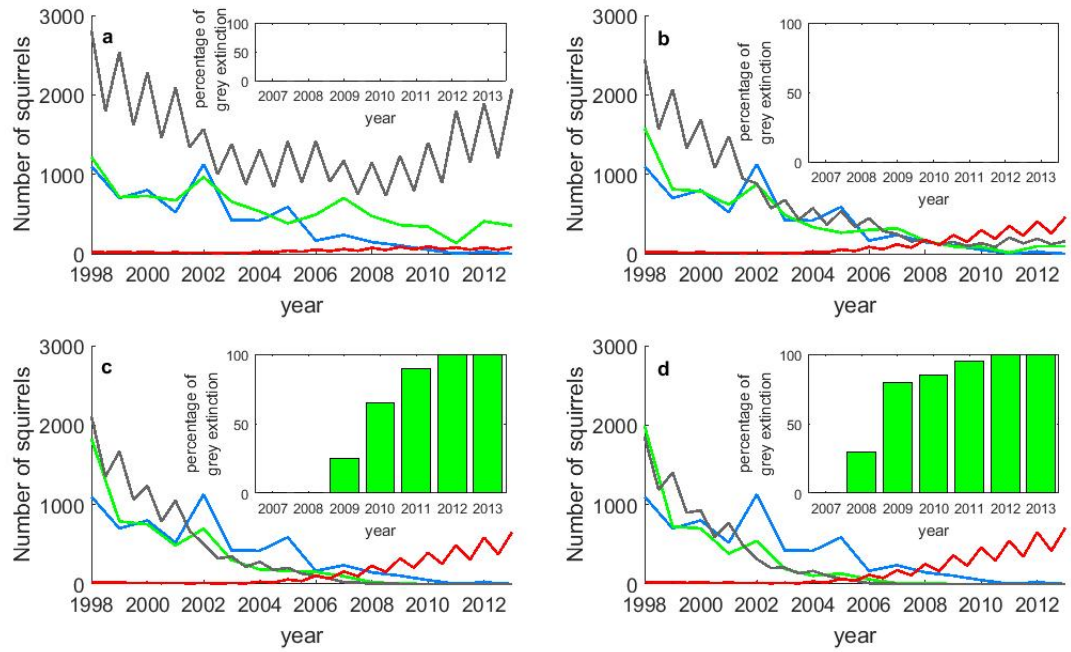


Figure 4.A.7: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under control strategy 2 with (a) $c=2.0$, (b) $c=3.0$, (c) $c=4.0$ and (d) $c=5.0$. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, $c=4.0$ and $c=5.0$ satisfy the criteria that 50% of realisations should show grey squirrel extinction between 2011-2013 (but not prior to this time) with the best fit statistics of $S=7448$ and $S=28404$ respectively.

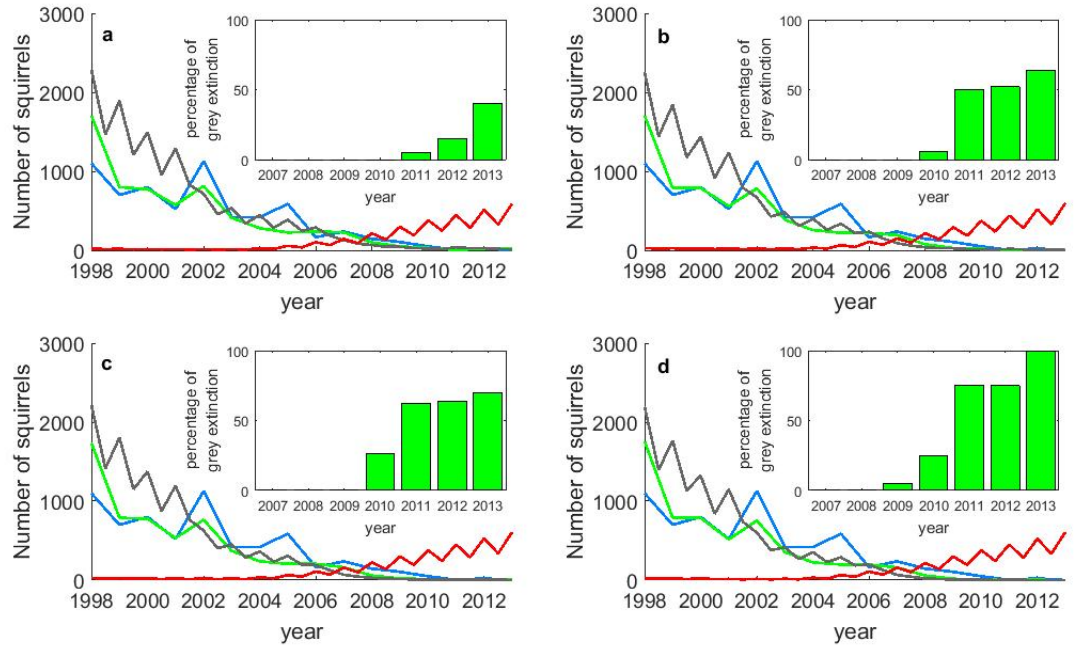


Figure 4.A.8: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under control strategy 2 with (a) $c=3.4$, (b) $c=3.5$, (c) $c=3.6$ and (d) $c=3.7$. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, $c=3.5$, $c=3.6$ and $c=3.7$ satisfy the criteria that 50% of realisations should show grey squirrel extinction between 2011-2013 (but not prior to this time) with the best fit statistics of $S=2072$, 3017 and 3609 respectively.

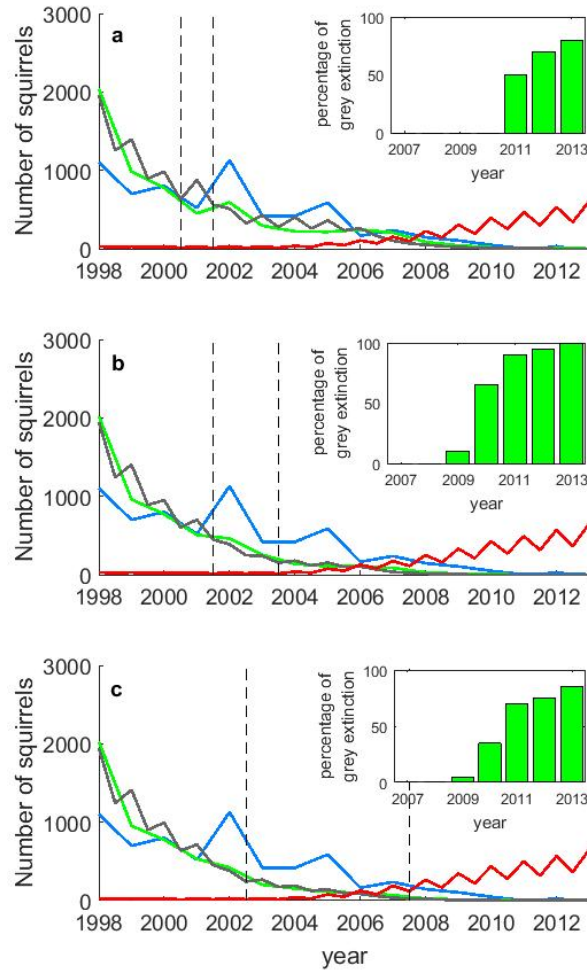


Figure 4.A.9: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 4.3) and those caught in the model under new trapping approach B with the change between stages triggered when the number of greys caught fell below (a) 50%, (b) 25% and (c) 10% of the initial number caught. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year.

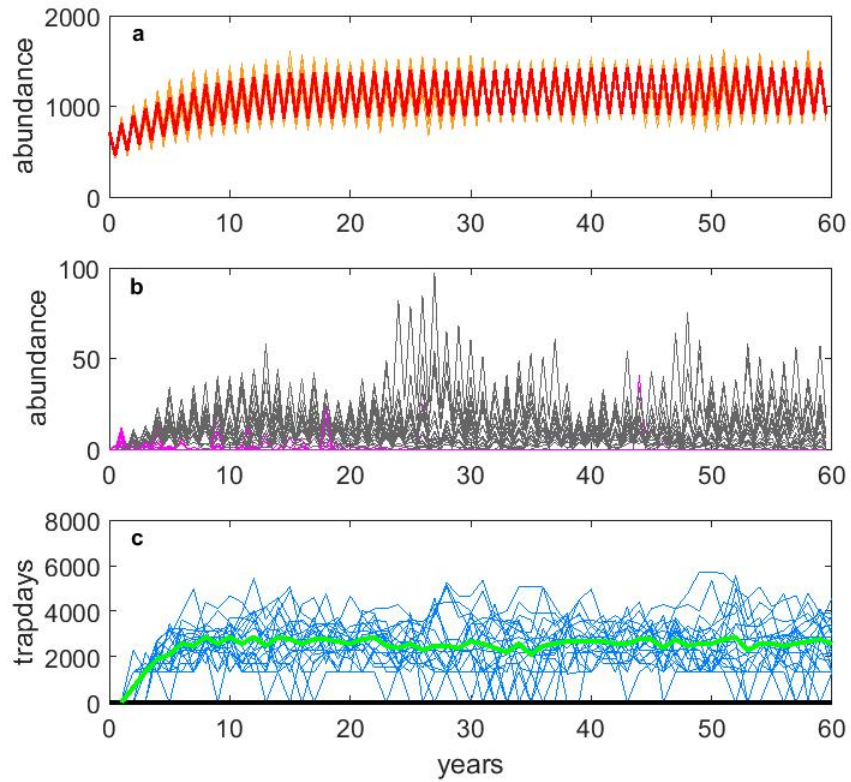


Figure 4.A.10: Model results for control method 1 shown in Table 4.5. Results show the output for all 20 model realisations with in (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line), on the mainland (black line) and the average total trapdays (green line). No control on the mainland occurs and control occurs for one month at T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

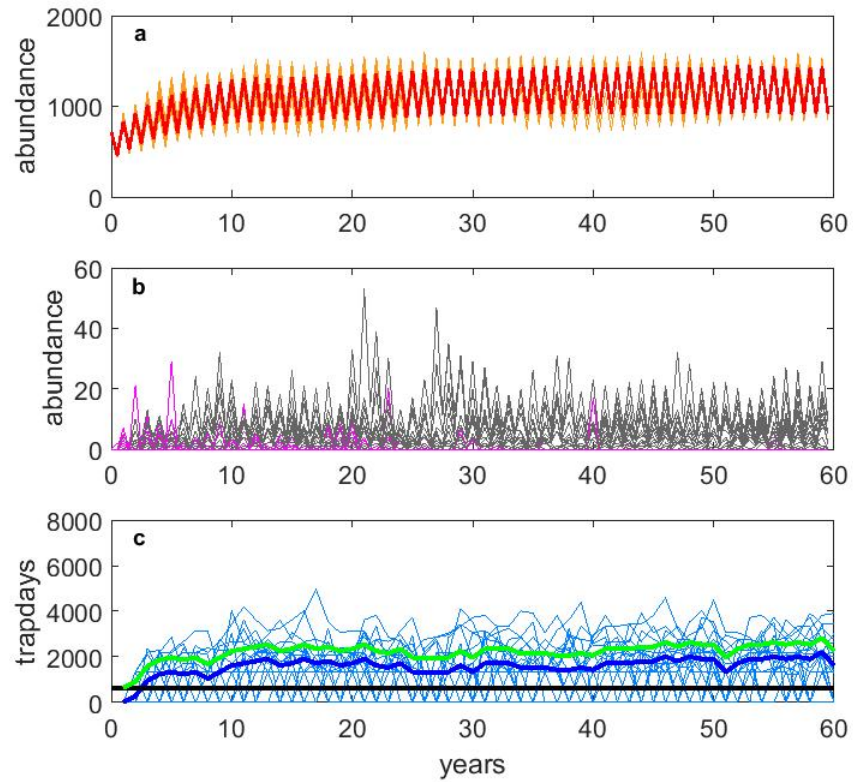


Figure 4.A.11: Model results for control method 2 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 10% of T_{max} and control occurs for one month at T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

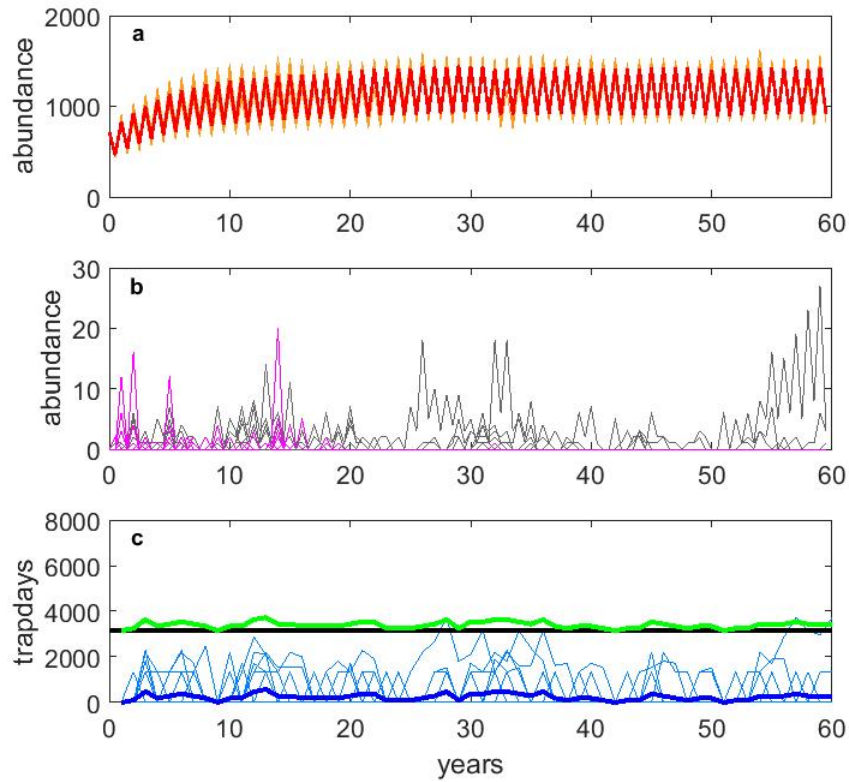


Figure 4.A.12: Model results for control method 3 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue - this shows that, in general, little control is required on Anglesey), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 50% of T_{max} and control occurs for one month at T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

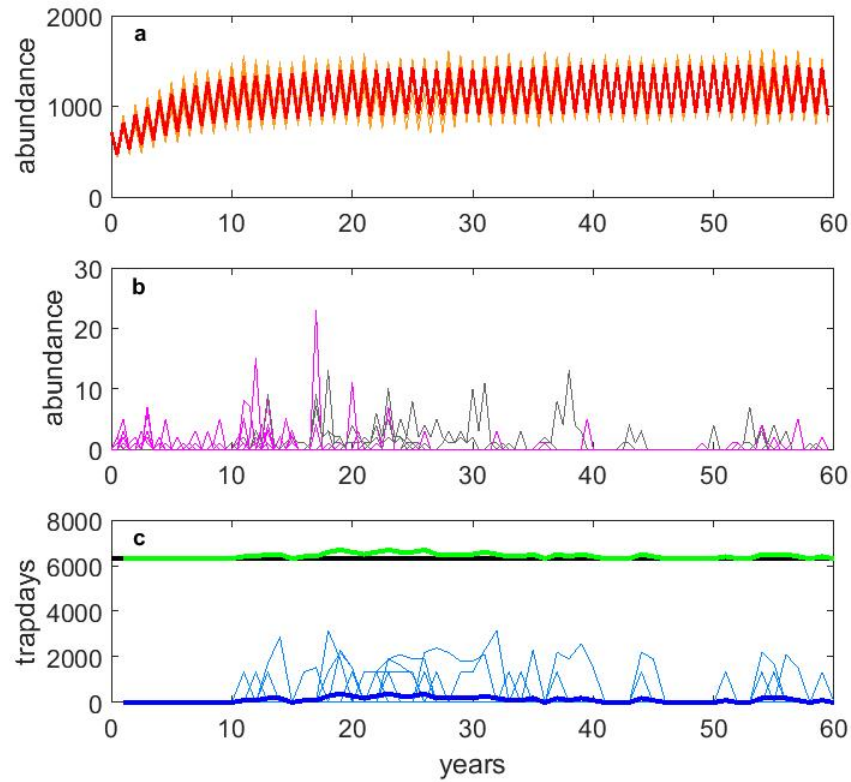


Figure 4.A.13: Model results for control method 4 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue - this shows that, in general, little control is required on Anglesey), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at T_{max} and control occurs for one month at T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

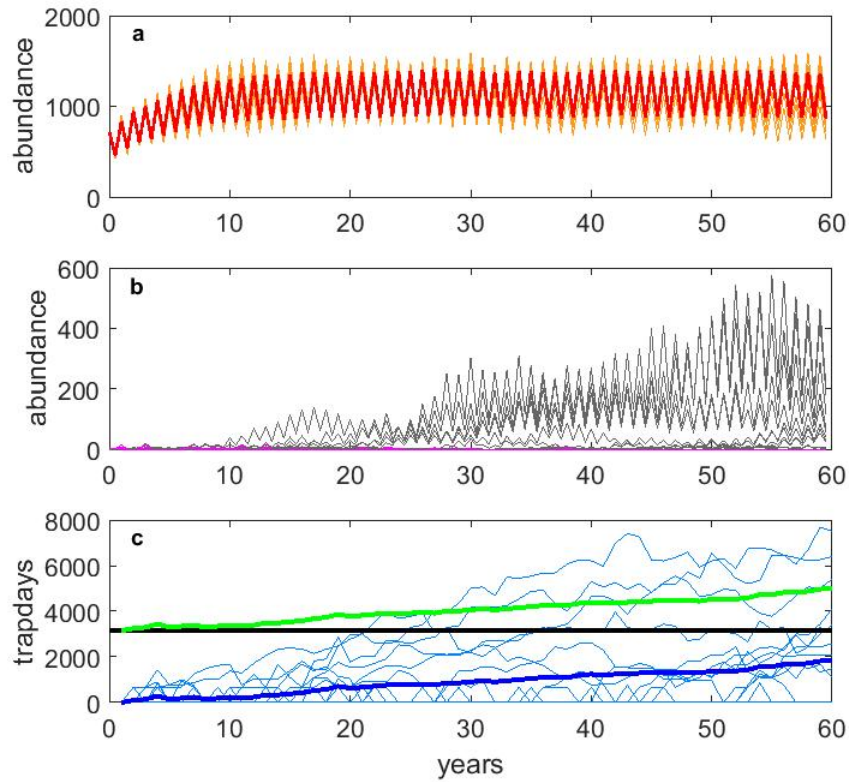


Figure 4.A.14: Model results for control method 5 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue - this shows that, in general, little control is required on Anglesey), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 50% of T_{max} and control occurs for one month at 50% of T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

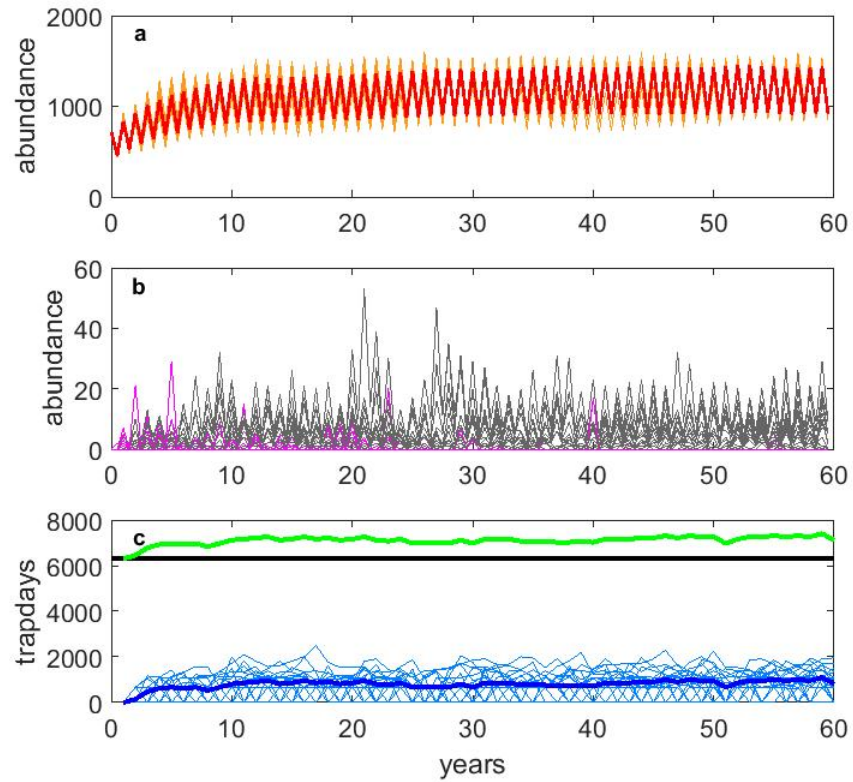


Figure 4.A.15: Model results for control method 6 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at T_{max} and control occurs for one month at 50% of T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

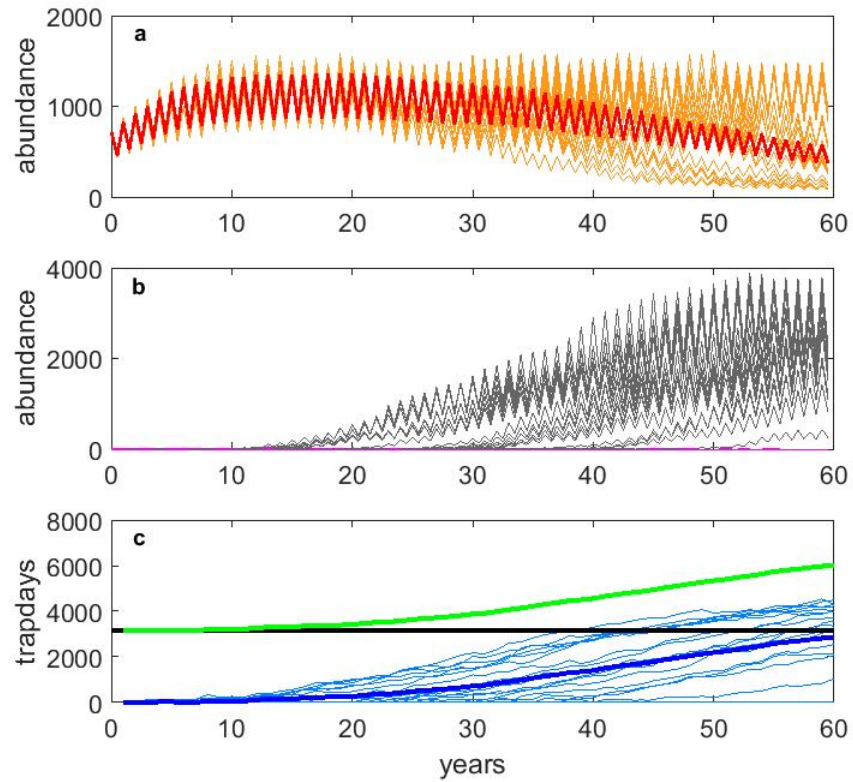


Figure 4.A.16: Model results for control method 7 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 50% of T_{max} and control occurs for one month at 10% of T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

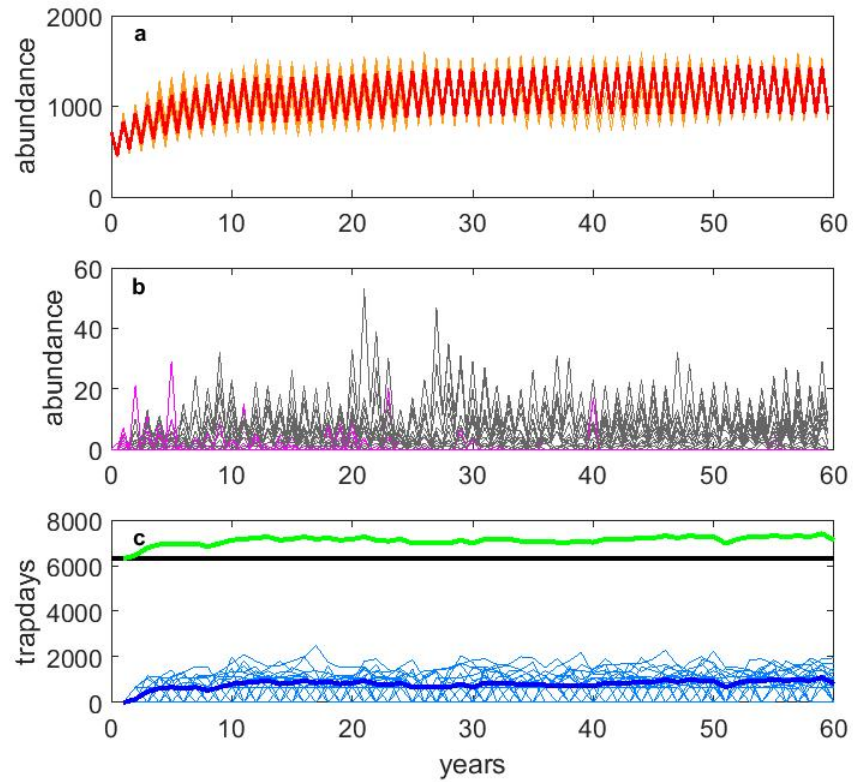


Figure 4.A.17: Model results for control method 8 shown in Table 4.5. Results show the output for all 20 model realisations with (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at T_{max} and control occurs for one month at 10% of T_{max} in grid cells (and those in a 2 km buffer around them) in which grey squirrels are present on Anglesey.

Chapter 5

The Impact of Stochasticity on Disease-Mediated Invasion

5.1 Introduction

It is well recognised that infectious disease is an important determinant in invasive species success in many ecological and biological systems (Daszak et al., 2000; Hudson and Greenman, 1998; Prenter et al., 2004). Indeed, infectious disease has played a key role in human history and the success of human movements and invasions across the globe. For instance, infectious disease may hinder invasion, such as when malaria contracted by invading British forces aided Washington's victory in Yorktown, Virginia, USA (McNeill, 2010). Infectious disease may also promote invasion, such as when European travellers to the Americas in the 15th century introduced smallpox to native populations that had no resistance to the disease. The disease carried by the invading Europeans acted like a 'biological weapon' and spread throughout the native populations, mediating the invasion of the Europeans (Diamond, 2005; Strauss et al., 2012).

Infectious disease can therefore have a range of consequences for invasion success which have been well documented in ecological literature (Strauss et al., 2012; Dunn and Hatcher, 2015). There are several scenarios that benefit the native species. When an invading species is susceptible to infectious disease that is endemic in the native community but pathogenic to the invader, it may prevent invasive species establishment (Hilker et al., 2005; Petrovskii et al., 2005). If the endemic parasites in the native species community do not prevent invasive establishment, the invader can share the disease with the native species. When the invader is a poor reservoir for the disease, it can reduce the disease prevalence, thereby aiding the native species by the 'dilution effect' (Ostfeld and Keesing, 2000; Keesing et al., 2006). Shared disease can benefit the invading species in several scenarios, termed disease mediated

invasion (DMI). If the parasite is less virulent in the invading species it may act as a carrier of the disease, increasing the overall prevalence and thus increasing mortality in the native species (known as spillback DMI), (Eppinga et al., 2006; Strauss et al., 2012). The invading species may introduce a parasite to the non-resistant native community. The introduction of a virulent disease increases mortality in the native species and leads to spillover DMI (Mitchell and Power, 2003; Strauss et al., 2012).

Mathematical modelling can be used to facilitate the understanding of the complexities in disease-mediated invasions. It has been used to explain why disease may prevent invasion success (Hilker et al., 2005), to detail the dilution effect (Keesing et al., 2006), to formulate the disease spillback hypothesis (Eppinga et al., 2006) and to highlight DMI through disease spillover (Tompkins et al., 2003). A key result relating to spillover DMI was presented in Bell et al. (2009). A general deterministic framework was used to show that a spillover DMI may lead to the spread of infection through the native species in advance of the spread of the invading species (a wave of disease is followed by a wave of replacement). This wave of infection causes disease induced mortality in the native species, reducing it to its endemic level and so increasing the rate of spread of the invader due to disease mediated apparent competition. These results suggested that the management of infectious disease may be crucial to protecting native species threatened by invasions.

The findings of Bell et al. (2009) informed a key case study system in which spillover DMI has been reported - namely the replacement of native red squirrels by invasive grey squirrels in the UK. Here, grey squirrels carry the shared disease squirrelpox which is harmless to grey squirrels but highly virulent to red squirrels. The speed of replacement of red squirrels is greatly increased by the presence of the disease (Tompkins et al., 2003; Rushton et al., 2006) and as reported by Bell et al. (2009), there is evidence that the disease occurs in advance of the spread and invasion of grey squirrels (Chantrey et al., 2014; White et al., 2016a). However, spatially realistic, stochastic models of the spread of squirrelpox have questioned whether the infection will spread extensively through the red only populations in advance of grey squirrel invasion (Macpherson et al., 2016a; White et al., 2016b; Jones et al., 2016). In these studies, local epidemics of squirrelpox were observed in red populations adjacent to endemic grey squirrel populations (or in a local neighbourhood following disease introduction), but due to the high virulence of the disease in red squirrels, the disease faded out before it could spread extensively. While the deterministic approach of Bell et al. (2009) provided key insight into the spatial outcomes of DMI, it could not consider disease fade-out. In this chapter we therefore consider a stochastic model framework as this can include the chance of extinction when population levels become small and can therefore represent the possibility of disease fade-out (Durrett and Levin, 1994; Hess, 1996). We intend to revisit the results

of Bell et al. (2009) using a stochastic model system that is the analogue of the deterministic system used in the Bell et al. (2009) study. We will characterise the situations in which the wave of disease followed by a wave of replacement occurs (as in Bell et al. (2009)) and also detail the conditions and population dynamics when this result does not occur due to stochasticity. We will discuss the consequences of the findings in relation to the threat of DMI from grey squirrels in the UK.

5.2 Methods

In this chapter we develop a stochastic model framework that corresponds to the deterministic model of Bell et al. (2009). For clarity we outline the model of Bell et al. (2009) in which the density of susceptibles, S_i , and infecteds, I_i , where $i = 1, 2$ with 1 being the native species and 2 being the invading species are represented as follows

$$\begin{aligned} \frac{\partial S_1}{\partial t} = & [a_1 - q_1(H_1 + c_2 H_2)]H_1 - b_1 S_1 \\ & - \beta_{11} S_1 I_1 - \beta_{12} S_1 I_2 + \gamma_1 I_1 + D_1 \frac{\partial^2 S_1}{\partial x^2} \end{aligned} \quad (5.1)$$

$$\frac{\partial I_1}{\partial t} = \beta_{11} S_1 I_1 + \beta_{12} S_1 I_2 - b_1 I_1 - \alpha_1 I_1 - \gamma_1 I_1 + D_1 \frac{\partial^2 I_1}{\partial x^2} \quad (5.2)$$

$$\begin{aligned} \frac{\partial S_2}{\partial t} = & [a_2 - q_2(H_2 + c_1 H_1)]H_2 - b_2 S_2 \\ & - \beta_{22} S_2 I_2 - \beta_{21} S_2 I_1 + \gamma_2 I_2 + D_2 \frac{\partial^2 S_2}{\partial x^2} \end{aligned} \quad (5.3)$$

$$\frac{\partial I_2}{\partial t} = \beta_{22} S_2 I_2 + \beta_{21} S_2 I_1 - b_2 I_2 - \alpha_2 I_2 - \gamma_2 I_2 + D_2 \frac{\partial^2 I_2}{\partial x^2} \quad (5.4)$$

$$\text{where } H_1 = S_1 + I_1 \quad \text{and} \quad H_2 = S_2 + I_2.$$

Here, a_i represents the maximum reproduction rate, b_i the natural mortality rate, c_i the competition effect of species i on the other species and β_{ij} the disease transmission coefficient from species j to i (in this study we let $\beta_{ij} = \beta$ for all i, j). The carrying capacity K_i is related to susceptibility to crowding, q_i , with $K_i = (a_i - b_i)/q_i$. α_i represents the rate of disease induced mortality (virulence) and γ_i is the rate at which infecteds may recover back to the susceptible class. Movement is represented by diffusion with diffusion coefficients D_1 and D_2 for species 1 and 2 respectively (which are not affected by infection status). As in Bell et al. (2009), we assume that

$$D_1 = D_2 = D.$$

To generate a stochastic model, we convert the rates in the deterministic model to probabilities of events following the methods of Gillespie (1977) (see also Renshaw (1991)). The events and associated probabilities are shown in Table 5.1. For the spatial set-up in the stochastic model, we assume a line of 1km by 1km grid squares. The grid cell size has been used successfully in previous studies of the red/grey squirrel system in the UK (White et al., 2014, 2016a; Macpherson et al., 2016a; Jones et al., 2016). To convert the diffusion term in the deterministic model into the probability of an individual moving to a neighbouring grid cell, we use the conversion outlined by Laing and Lord (2009) (also see Erban et al. (2007)) which is as follows:

$$d = \frac{2D}{h^2} \quad (5.5)$$

where d is the rate of leaving the current patch, $h = 1$ is the patch width and the multiplying factor of 2 is required as there is a chance of dispersal occurring to the left or right grid square in the random walk process represented by diffusion (Laing and Lord, 2009).

The events in Table 5.1 are implemented at random with the associated probabilities updated after each event. The time between events is given by the exponentially distributed random variable $T_{\text{event}} = -\ln(\sigma)/R$ where σ is a random number from the uniform distribution, $[0, 1]$ (Renshaw, 1991). Using Fortran 90, a Gillespie algorithm is used to obtain individual simulations and provide information of the behaviour in a single realisation (Renshaw, 1991). To determine the average behaviour and variability, multiple realisations are generated. We compare these stochastic results to deterministic results obtained using pdepe in Matlab to solve Equations 5.1-5.4.

Table 5.1: The stochastic model within each 1 km by 1 km grid square indicating the probability of different events occurring. Here $R = \sum[\text{rates}]$ (the sum of the rates in square brackets). The dispersal term is shown for the class S_1 only but is similar for all other classes. We assume an equal chance of dispersal to the left or right neighbouring patch (which increases the abundance in that patch by 1).

Birth of native to S_1	$P(S_1 \rightarrow S_1 + 1)$	$:[a_1 - q_1 (H_1 + c_2 H_2) H_1]/R$
Natural death of S_1	$P(S_1 \rightarrow S_1 - 1)$	$:[b_1 S_1]/R$
Infection of native	$P(S_1 \rightarrow S_1 - 1, I_1 \rightarrow I_1 + 1)$	$:[\beta S_1 (I_1 + I_2)]/R$
Recovery of native	$P(I_1 \rightarrow I_1 - 1, S_1 \rightarrow S_1 + 1)$	$:[\gamma_1 I_1]/R$
Death of I_1	$P(I_1 \rightarrow I_1 - 1)$	$:[(b_1 + \alpha_1) I_1]/R$
Birth of invasive to S_2	$P(S_2 \rightarrow S_2 + 1)$	$:[a_2 - q_2 (H_2 + c_1 H_1) H_2]/R$
Natural death of S_2	$P(S_2 \rightarrow S_2 - 1)$	$:[b_2 S_2]/R$
Infection of invasive	$P(S_2 \rightarrow S_2 - 1, I_2 \rightarrow I_2 + 1)$	$:[\beta S_2 (I_1 + I_2)]/R$
Recovery of invasive	$P(I_2 \rightarrow I_2 - 1, S_2 \rightarrow S_2 + 1)$	$:[\gamma_2 I_2]/R$
Death of I_2	$P(I_2 \rightarrow I_2 - 1)$	$:[(b_2 + \alpha_2) I_2]/R$
Dispersal of S_1	$P(S_1 \rightarrow S_1 - 1)$	$:[d S_1]/R$

We initially use parameter values outlined in Bell et al. (2009) and compare the deterministic and stochastic results. We then consider a range of alternative parameters that highlight the differences in the results between the deterministic and stochastic versions of the model.

5.3 Results

5.3.1 Comparison of stochastic model and deterministic model for the parameters in Bell et al. (2009)

To provide some background understanding, we initially compare the results of the stochastic and deterministic versions of the model for the parameters of Bell et al. (2009). The deterministic model reproduces the key result from Bell et al. (2009) and shows that a wave of disease travels in advance of a wave of replacement (Figure 5.1). The wave of disease transforms the native species from its disease-free level to its endemic level and the wave of replacement transforms the native species at its endemic level to the invading species at its endemic level. We find that the stochastic and deterministic set-up show similar results (Figure 5.1). In particular, the two distinct waves can occur in the stochastic set-up. Individual realisations show some variation, due to unsuccessful invasion attempts at the wave fronts, but

on average there is good agreement between the stochastic and deterministic models. In the deterministic system, this result holds when the disease can be supported at endemic levels in both species and when the invader has a competitive advantage when the disease is present. For the parameters used in Bell et al. (2009), this is also the case in the stochastic model (Figures 5.2-5.4). Next, we examine whether this results holds in the stochastic system for all the parameter values under which it holds in the deterministic system.

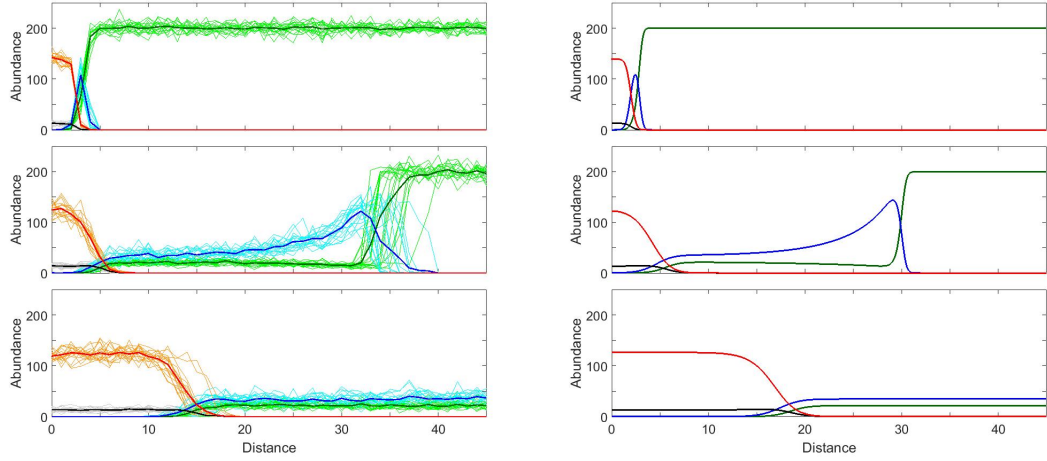


Figure 5.1: The dynamics of the models when susceptible and infected non-natives are introduced into a disease-free native species: A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average abundances shown in bold) and the deterministic model (right) when susceptible and infected non-natives are introduced into a disease-free native species (using the parameters of Bell et al. (2009)). The infected native population is shown by the blue lines, the susceptible native population by the green lines, the infected non-native population by the red lines and the susceptible non-native population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which it is at the endemic non-native steady state. The parameters are: $a_1 = a_2 = 1$, $b_1 = b_2 = 0.4$, $K_1 = K_2 = 200$, $c_1 = 0.9$, $c_2 = 1.5$, $\alpha_1 = 0.7$, $\alpha_2 = 0.2$, $\gamma_1 = \gamma_2 = 0.2$, $\beta = 0.06$ and $D = 0.18$.

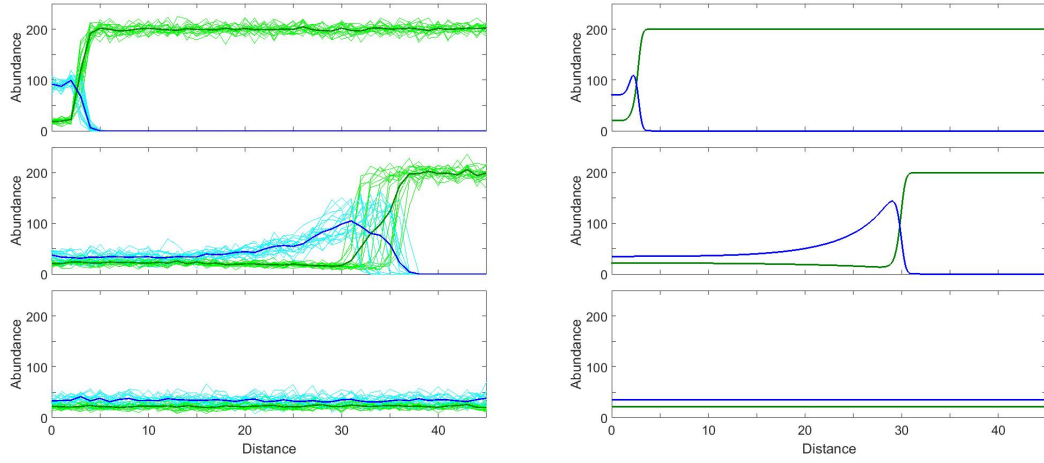


Figure 5.2: The dynamics of the models when infection is introduced into a disease-free native species (Bell et al. (2009) parameters): A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average abundances shown in bold) and the deterministic model (right) when infection is introduced into a disease-free native species (using the parameters of Bell et al. (2009)). The infected population is shown by the blue lines and the susceptible population by the green lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which the population is at the native endemic steady state. The parameters are: $a_1 = 1$, $b_1 = 0.4$, $K_1 = 200$, $\alpha_1 = 0.7$, $\gamma_1 = 0.2$, $\beta = 0.06$ and $D = 0.18$.

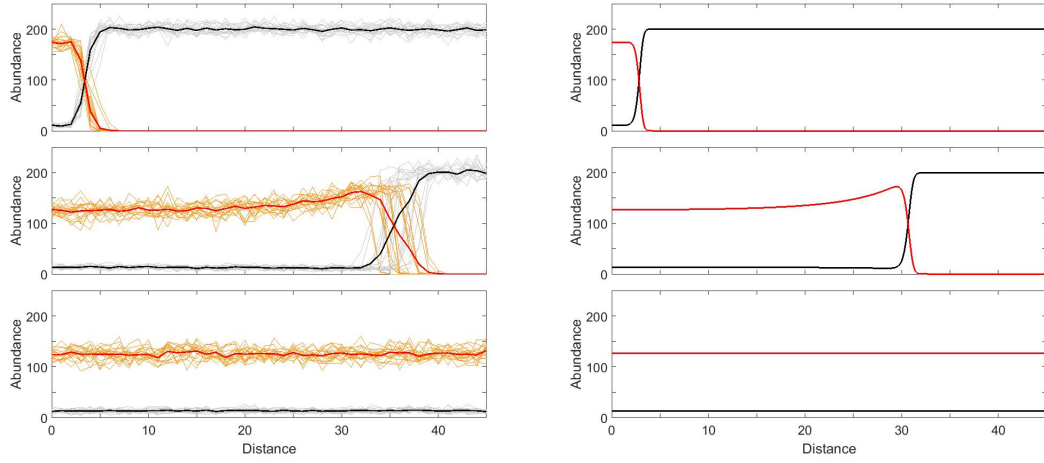


Figure 5.3: The dynamics of the models when infection is introduced into a disease-free non-native species (Bell et al. (2009) parameters): A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average abundances shown in bold) and the deterministic model (right) when infection is introduced into a disease-free non-native species (using the parameters of Bell et al. (2009)). The infected population is shown by the red lines and the susceptible population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the non-native species is at its carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which the population is at the non-native endemic steady state. The parameters are: $a_2 = 1$, $b_2 = 0.4$, $K_2 = 200$, $\alpha_2 = 0.2$, $\gamma_2 = 0.2$, $\beta = 0.06$ and $D = 0.18$.

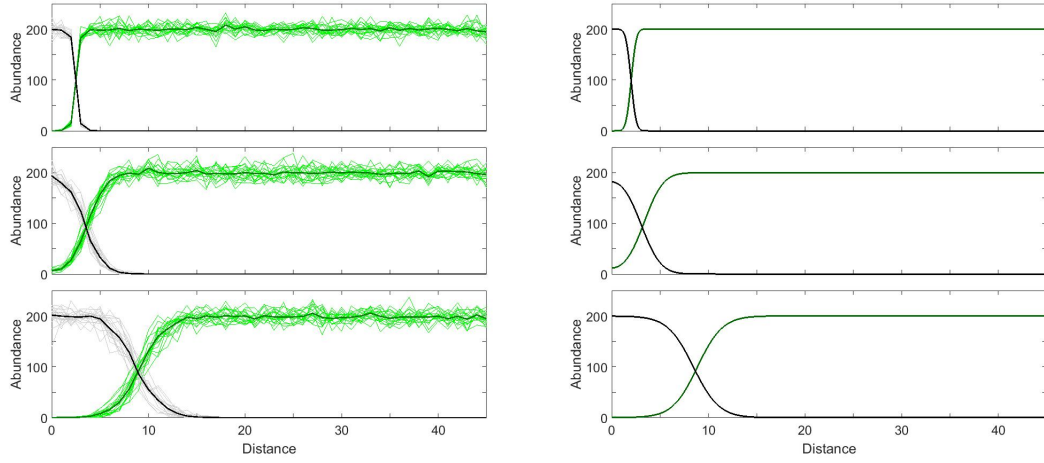


Figure 5.4: The dynamics of the models when a disease-free non-natives is introduced into a disease-free native species (Bell et al. (2009) parameters): A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average abundances shown in bold) and the deterministic model (right) when a disease-free non-native species is introduced into a disease-free native species (using the parameters of Bell et al. (2009)). The susceptible native population is shown by the green lines and the susceptible non-native population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which the non-native species is at its carrying capacity. The parameters are: $a_1 = a_2 = 1$, $b_1 = b_2 = 0.4$, $K_1 = K_2 = 200$, $c_1 = 0.9$, $c_2 = 1.5$ and $D = 0.18$.

5.3.2 Disease persistence in the stochastic model

A key requirement for the wave of disease followed by a wave of replacement in Bell et al. (2009) is that the disease can persist in the native and invading species. We assess the range of parameters under which the disease can persist in the deterministic and stochastic models. Figure 5.5 indicates the parameter combinations in terms of disease virulence (α) and recovery (γ) that allow disease persistence (below the lines) or in which the disease is not supported (above the lines) for the deterministic (red) and stochastic (blue) models. For the parameters used in Figure 5.2 ($\alpha_1 = 0.7$, $\gamma_1 = 0.2$) and in Figure 5.3 ($\alpha_2 = 0.2$, $\gamma_2 = 0.2$), the disease can persist under both model set-ups. However, there is a region between the red and blue lines in Figure 5.5 in which the disease persists in the deterministic model but fades-out in the stochastic model. The spatial dynamics of the system with parameters in this region are shown in Figure 5.6. In the deterministic model a wave of disease transforms the population to the endemic level (albeit with a very low density of infecteds). In

the stochastic model the disease spreads locally in the neighbourhood of the point of introduction but then fades-out and so the disease does not spread extensively across the landscape. The population therefore returns to its disease-free level across the landscape. More generally, Figure 5.5 indicates that the disease persists in the stochastic model for low levels of virulence and recovery as here, individuals spend a substantial time in the infected class (and so can infect others). If the recovery rate becomes too high, or if virulence becomes too high then infected individuals are lost from the infected class more rapidly (through recovery or disease induced mortality respectively). This reduces the chance of secondary infections and causes the disease to fade out in the stochastic model.

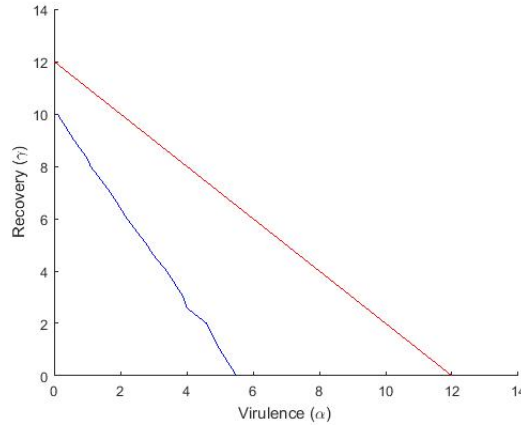


Figure 5.5: A graph indicating when the disease can persist (below the line) for the deterministic (red) and stochastic (blue) model. Persistence for the deterministic model occurs when $R_0 = \beta K / (\alpha + \gamma + b) = 1$. We assume that persistence occurs for the stochastic model if the disease is present after 60 years in a least 50% of the model realisations.

In the next section, we consider the outcome of invasion for a range of scenarios when the disease can and cannot persist in the native or the invading species.

5.3.3 Invasion success in the stochastic model

When the disease can persist in both the native and invading species, the outcome of the stochastic and deterministic models is similar and produces the results reported in Bell et al. (2009), shown in Figure 5.1. We now consider the situation in which disease can persist in the invading species but would fade-out in the native species. The results are reported in Figure 5.7 and show clear differences between the deterministic and stochastic set-ups. The deterministic model shows a wave of disease followed by a wave of replacement as in Figure 5.1. In the stochastic model however, the wave of disease is absent and there is only a wave of replacement which

transforms the native species at its disease-free level to the invading species at its endemic level. The wave of disease is absent due to the high virulence of the disease which leads to stochastic fade-out of infection and the failure of the disease to spread extensively through the native population. The disease does however play a key role in the rate of spread of the invasive species. In particular, the wave of replacement in Figure 5.7 is more rapid than that in Figure 5.4 in which the disease is absent. Even though the disease cannot be supported in the native species, its persistence in the invading species leads to epidemic outbreaks in the native species at the wave front (Figure 5.8). This reduces the density of the native species at the wavefront (the interface between the native and invading species) and therefore reduces the competitive ability of the native and so mediates invasion. This is a key result and suggests that even when a disease cannot persist in the native species (due to stochastic fade-out), it can still play a key role in enhancing the replacement of native species through disease mediated invasion.

For completeness, we consider parameters of the stochastic system for which the disease can persist in the native species but not in the invading species and when the disease cannot persist in either species. In Figure 5.9, we consider an endemic (low virulence) disease in the native species and then introduce the invading species that suffers high virulence from the disease. Here, for both the deterministic and stochastic system, the persistence of the disease in the native system causes high mortality in the invading species and so the invader fails to establish despite the invasive species having a competitive advantage in the absence of the disease. This supports the findings of earlier theoretical studies (Hilker et al., 2005; Petrovskii et al., 2005) which report that pathogens can reverse the invasion fronts of hosts or lead to patchy patterns of invasion. In Figure 5.10, the disease cannot be supported in either the native or invader in the stochastic system and so the disease fades-out. The stochastic system therefore shows competitive replacement of the native species in the absence of the disease (as in Figure 5.4). The deterministic system shows a wave of disease followed by a wave of replacement (as in Figure 5.1).

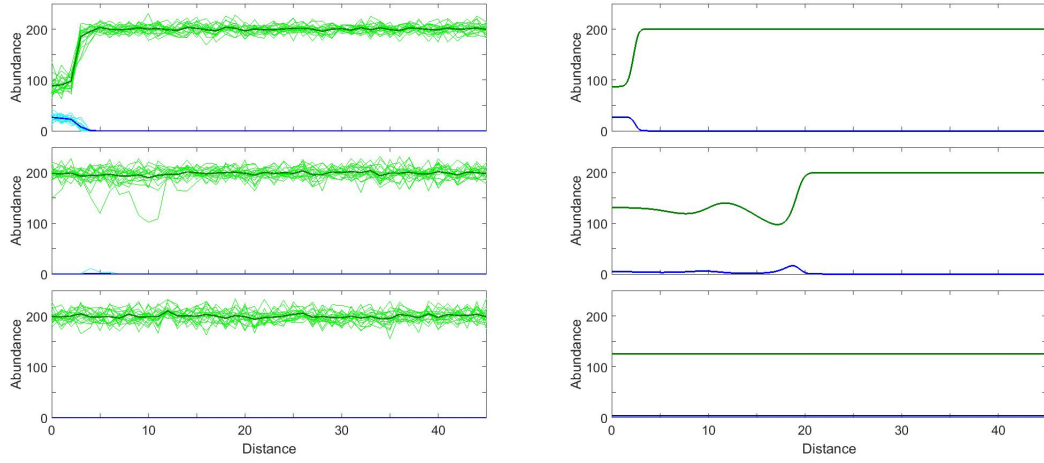


Figure 5.6: The dynamics of the models when infection is introduced into a disease-free native species (with high a disease induced death rate and no recovery from the disease): A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average shown in bold) and the deterministic model (right) when infection is introduced into a disease-free native species. The infected population is shown by the blue lines and the susceptible population by the green lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its disease-free carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which it is at the endemic native steady state. The parameters are: $a_1 = 1$, $b_1 = 0.4$, $K_1 = 200$, $\alpha_1 = 7.14$, $\gamma_1 = 0$, $\beta = 0.06$ and $D = 0.18$.

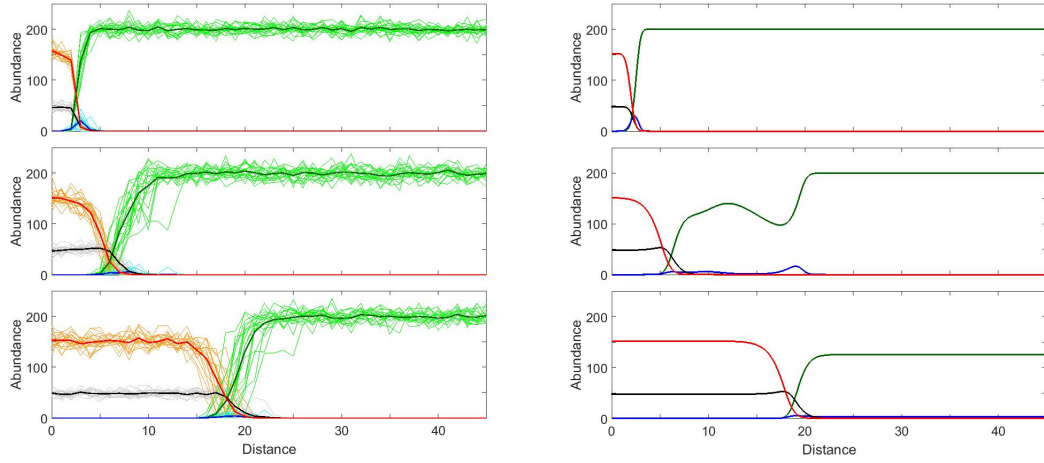


Figure 5.7: The dynamics of the models when susceptible and infected non-natives are introduced into a disease-free native species in which the disease is highly virulent and there is no recovery from: A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average shown in bold) and the deterministic model (right) when susceptible and infected non-natives are introduced into a disease-free native species. The infected native population is shown by the blue lines, the susceptible native population by the green lines, the infected non-native population by the red lines and the susceptible non-native population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its carrying capacity in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which it is at the endemic non-native steady state. The parameters are: $a_1 = a_2 = 1$, $b_1 = b_2 = 0.4$, $K_1 = K_2 = 200$, $c_1 = 0.9$, $c_2 = 1.5$, $\alpha_1 = 7.14$, $\alpha_2 = 0$, $\gamma_1 = 0$, $\gamma_2 = 2.47$, $\beta = 0.06$ and $D = 0.18$.

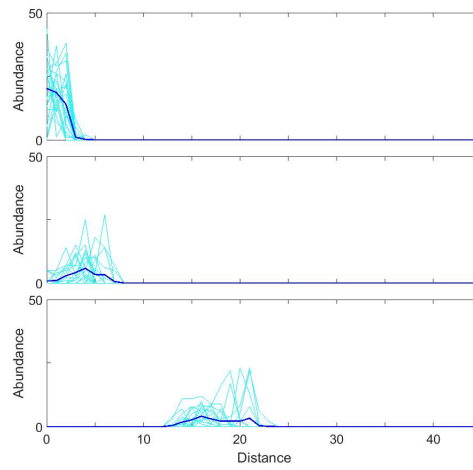


Figure 5.8: The abundance (and average abundance shown in bold) of the infected native population for the 20 model realisations shown in Figure 5.7. The model set up is described in Figure 5.7.

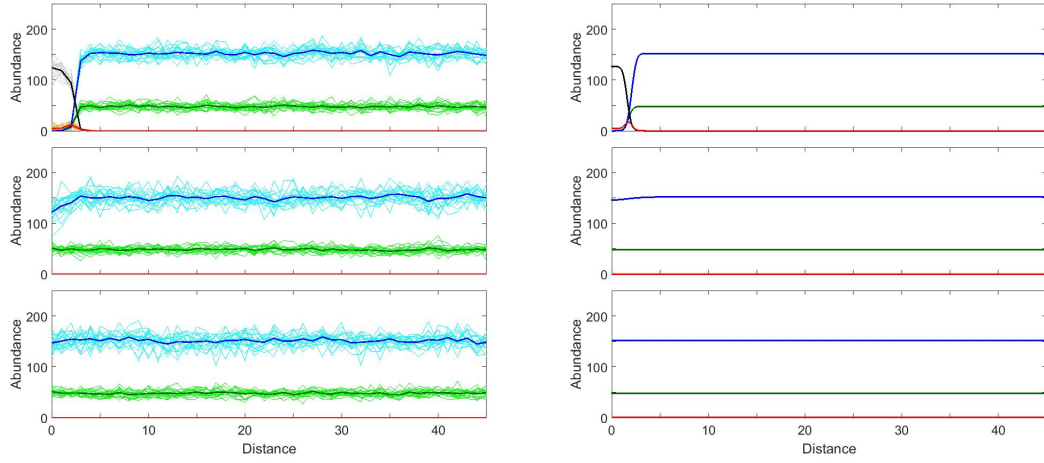


Figure 5.9: The dynamics of the models when non-natives (to which the disease is highly virulent) are introduced into a native species with disease at the endemic state: A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average shown in bold) and the deterministic model (right) when non-natives are introduced into a native species at the disease endemic state. The infected native population is shown by the blue lines, the susceptible native population by the green lines, the infected non-native population by the red lines and the susceptible non-native population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its disease endemic state in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which it is at the endemic non-native steady state. The parameters are: $a_1 = a_2 = 1$, $b_1 = b_2 = 0.4$, $K_1 = K_2 = 200$, $c_1 = 0.9$, $c_2 = 1.5$, $\alpha_1 = 0$, $\alpha_2 = 7.14$, $\gamma_1 = 2.47$, $\gamma_2 = 0$, $\beta = 0.06$ and $D = 0.18$.

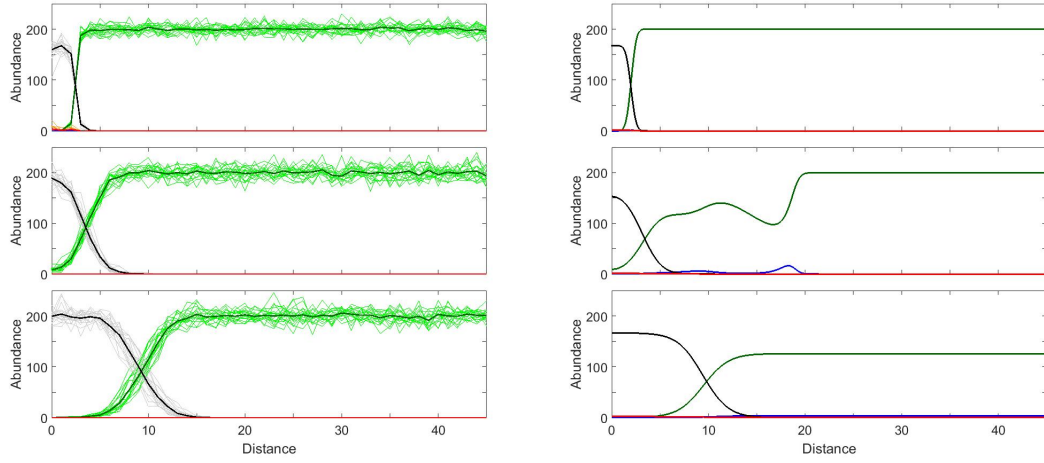


Figure 5.10: The dynamics of the models when susceptible and infected non-natives are introduced into a disease-free native species with the disease being very virulent in both species: A comparison of the dynamics of the stochastic model (left, 20 model realisations are run with the average shown in bold) and the deterministic model (right) when susceptible and infected non-natives are introduced into a disease-free native species. The infected native population is shown by the blue lines, the susceptible native population by the green lines, the infected non-native population by the red lines and the susceptible non-native population by the black lines. The abundances are shown after 1 year (top), 10 years (middle) and 40 years (bottom). Initially the native species is at its disease-free state in the spatial domain of 45 linear 1km by 1km grid cells except for in the 3 left grid cells in which it is at the endemic non-native steady state. The parameters are: $a_1 = a_2 = 1$, $b_1 = b_2 = 0.4$, $K_1 = K_2 = 200$, $c_1 = 0.9$, $c_2 = 1.5$, $\alpha_1 = 7.14$, $\alpha_2 = 7.14$, $\gamma_1 = 0$, $\gamma_2 = 2.47$, $\beta = 0.06$ and $D = 0.18$.

5.4 Discussion

Stochastic models of ecological populations are important in situations where population levels become low to account for the chance of stochastic extinction. This is particularly relevant when considering invasive systems as stochastic frameworks provide essential realism when abundance is low and so can account for unsuccessful invasion or the fade-out of infection. We have examined whether spillover DMI, reported by Bell et al. (2009) for a deterministic model framework, due to the interaction between a disease carrying invading and native species, occurs in the equivalent stochastic framework. Our results confirm that the introduction of a virulent disease increases mortality in the native species and can lead to spillover DMI (Mitchell and Power, 2003). This process could underpin many reported examples in the ecological literature (for a review see Strauss et al. (2012); Dunn and

Hatcher (2015)). Our results therefore have implications for the threat posed by the introduction of disease carrying invaders to the conservation and diversity of native species.

A well-documented example of DMI is the replacement of red squirrels by grey squirrels in the UK. Grey squirrels carry squirrelpox that causes high mortality in reds. Red replacement by greys has been reported to be more rapid in regions where squirrelpox is present in greys (Tompkins et al., 2003; Rushton et al., 2006). The studies by Tompkins et al. (2003) and Bell et al. (2009) suggested that the spread of squirrelpox through populations of red squirrels in advance of the invading greys could potentially explain the rapid replacement of reds. While outbreaks of squirrelpox in red populations have been reported in regions local to grey squirrels (Chantrey et al., 2014), the wide ranging spread and persistence of squirrelpox has not been observed through red-only populations. Spatially realistic models of the red-grey-squirrelpox system have also reported that squirrelpox can lead to local epidemics and high mortality in reds but suggested that squirrelpox would not be supported within red-only populations as the disease would fade-out before spreading extensively through red-only populations at the landscape scale (Lurz, 2015; White et al., 2016b; Jones et al., 2016). These latter results seem to contradict the suggestions of Tompkins et al. (2003) and Bell et al. (2009) and question whether squirrelpox is a key factor in the rapid replacement of red squirrels.

Our results (Figure 5.7) help resolve this potential conflict. The parameters here are chosen to reflect the key processes in the UK squirrel system. The invader does not suffer disease induced mortality and can recover from infection, while the virulence is high for the native which cannot recover from the disease. We also set the basic reproductive ratio (R_0) of the disease for the native and invader to match the levels for red and grey squirrels used in Tompkins et al. (2003). Our stochastic model shows that while the disease does not spread extensively through the native population, the disease does persist in the invading species and epidemic outbreaks of infection that lead to high levels of mortality occur locally at the invasive front (the interface between the native and the invader). The impact of disease at the wavefront leads to spillover DMI and results in more rapid spread and replacement than in the absence of the disease. This may explain why squirrelpox is not widespread in red squirrel only populations but also why its presence in grey squirrels coincides with a greater rate of red replacement by grey squirrels. There are other examples in which spillover DMI occurs without the extensive spread of disease through the native system (Strauss et al., 2012; Dunn and Hatcher, 2015). For instance, in Europe crayfish plague (caused by the fungus *Aphanomyces astaci*) which was introduced with the invasive signal crayfish (*Pacifastacus leniusculus*) lead to spillover DMI and extinction of the native white clawed crayfish (*Austropotamobius pallipes*). However,

when the fungal disease emerged in Ireland, without the invader acting as a reservoir, the disease faded out after a local epidemic (Dunn and Hatcher, 2015). This adds further support to the findings reported in this study.

Spillover DMI requires that the disease persists in the invading species. Invasion dynamics can vary across different introduction regions with persistence, spread and prevalence all changeable (Goldstein et al., 2014). In the squirrel system, the distribution and composition of suitable habitat means that there is a large variation in the density of red and grey squirrels over the UK. Squirrelepox is likely to be of most significance in high density, good habitat regions, and may explain the rapid spread through southern and central England in broad-leaf dominated habitat. In Scotland, Wales and Ireland, the density is lower and squirrelepox may not be supported in grey squirrels or may show variations in prevalence (Goldstein et al., 2014; Jones et al., 2016). Our results (Figure 5.10) show that if the disease is not supported in the invading species then replacement is due to competition only. In the case of squirrelepox, Jones et al. (2016) reported that the low density of grey squirrel populations near Anglesey may fail to support squirrelepox at endemic levels and therefore that competition alone is the main driver of red squirrel replacement on Anglesey. The general results reported here support this finding.

It is important to note that the key result of Bell et al. (2009) is still valid in many situations where disease persists in both the invading and native species. Here the disease is predicted to spread extensively through the native species. For example, the emerging pathogenic fungus *Batrachochytrium dendrobatidis* causes chytridiomycosis infection in amphibians which has been linked to numerous species declines and extinctions in across the American continent, Australia and Europe (Berger et al., 1998; Garner et al., 2006; Bosch et al., 2001). It has been suggested that the disease may have been introduced with the escape or release of the farmed American bullfrog (*Rana catesbeiana*) which shows low mortality to the infection (Garner et al., 2006; Daszak et al., 2003). Following infection from the invasive host species, the disease has been reported to spread and persist in a range of native species (Garner et al., 2006). This supports the findings in Figure 5.1 and also highlights how invading species may be the source of emergent infectious disease (Dunn and Hatcher, 2015).

Chapter 6

Discussion

In this thesis we have developed mathematical modelling techniques to understand the invasion of a non-indigenous species and the potential threat it may have to native species. Our work uses classical modelling frameworks of species interaction and disease dynamics. Therefore, we can infer understanding to a wide range of systems in which native species are threatened by invaders. This is important as increased globalisation and climate change have resulted in an increase in the establishment of invasive species which often has negative effects on native species (Strauss et al., 2012; Dunn and Hatcher, 2015). Resources for management of invasive species are variable and limited - models provide invaluable predictions that help target and optimise the use of these funds.

With a rising number of non-indigenous species establishing in new areas, the impacts of the new species on the ecosystem systems must be evaluated to determine if the overall effect of the species is detrimental (Lundberg, 2010; McLaughlan et al., 2014). Invasive non-indigenous species that have a negative impact on native species can lead to biotic homogenization, with larger populations of single invading species dominating environments (Manchester and Bullock, 2000). However, non-indigenous species need not be removed or controlled if the positive benefits outweigh the negative impacts. Thus, intervention must be considered on a case by case basis (Lundberg, 2010; McLaughlan et al., 2014).

In this thesis, we have largely focused on the case study system of the invasion of grey squirrels and replacement of red squirrels in the UK. In much of the UK, red squirrels have been replaced by a process of disease-mediated invasion and without control strategies to limit the ongoing spread of grey squirrels, it is feared that red squirrels may become extinct on the mainland of the UK. Grey squirrels are also considered a major threat to native species in mainland Europe, particularly in Italy and the countries bordering it (Gurnell, 1996b; Bertolino and Genovesi, 2003; Bertolino, 2009). Beyond the threat from grey squirrels on red squirrels, they can also cause direct economic damage mostly due to bark stripping, reducing the value

of the timber (Shorten, 1954; Kenward and Parish, 1986). Preventing damage to trees to protect the quality of timber and therefore its financial value was the main motivation behind grey squirrel management until the 1990s (Gurnell and Pepper, 2016). Grey squirrel damage to agriculture has been reported in northern Italy, with grey squirrels damaging newly generated maize seedlings. This is of notable concern to British agriculture as grey squirrels are more populous in Britain and maize is a popular commercial crop (Signorile and Evans, 2006). Horticultural damage (e.g. digging up gardens and bulbs and eating fruit) is also a noted issue on a local scale (Gurnell, 1987). Grey squirrel damage to property in Britain is estimated to cost £1.9 billion annually due to problems such as the gnawing of electrical cables (on occasion leading to house fires) and damage to roofs (Gurnell, 1987; Williams et al., 2010). As a result of these detrimental impacts, grey squirrels have been classified as serious pests and have thus been listed by the World Conservation Union in “100 of the worst invasive alien species in the world” (Lowe et al., 2000). Moreover, under the 1981 Wildlife and Countryside Act, it is illegal to import, release or keep grey squirrels in Britain without a licence (Sheail, 1999).

In this discussion, we intend to review current intervention strategies that have been designed to reduce the impact that grey squirrels have on the environment. We will also discuss how the work we have undertaken can help inform the the best strategies that can be used to control grey squirrels.

6.1 Current Red Squirrel Conservation Strategies

There are two main strategies for protecting the remaining red squirrels in the UK from replacement by grey squirrels. In the highlands of Scotland there are extensive, continuous populations of red squirrels and protection is undertaken by controlling grey squirrels along the interface between red and grey squirrel populations on the “highland line” that runs from Loch Lomond in the west to Montrose in the east. Red squirrels persist in the absence of greys above this line and so reds are protected by preventing the range expansion of greys. Elsewhere in the UK, the conservation strategy is to protect red squirrels in stronghold/priority regions - areas of land that are managed to provide suitable habitat for red squirrels. There are 37 red squirrel strongholds in the UK, some of which have ongoing programmes of grey squirrel control in surrounding buffer areas. Of these, there are three large island strongholds (Isle of Anglesey, Isle of Wight and Isle of Arran) coupled with some smaller islands such as Brownsea and Tresco, Scilly Islands and mainland strongholds (Gurnell et al., 2016b). These strongholds are refuges from grey squirrels, with the island strongholds also protecting reds from the direct threat of disease-mediated invasion.

In some strongholds, the population abundance of red squirrels can be low and potentially drop below the 200 individuals which has been suggested as the minimum viable population size (Gurnell et al., 2002). This makes such stronghold populations susceptible to stochastic extinction (Gurnell et al., 2016a). The low population size can also make it difficult to maintain strong genetic diversity within the populations. Population abundance may be low as there may be other economic, recreational or conservation priorities also influencing the land use (Gurnell et al., 2004). For example, some of the strongholds are actively managed for commercial reasons (such as Kidland and Uswayford in Chapter 2). Therefore, the woodlands will be continually felled and replanted so the tree composition may not be ideal for red squirrels at times. By working directly with land management agencies, our modelling work has been able to test how red squirrel viability can be influenced by different management practices. We have been able to suggest methods by which red squirrel population abundance can be improved and these suggestions have been incorporated into the forest design plans that have been proposed by Forestry Commission England for Kidland and Uswayford.

There have been several attempts to eradicate grey squirrels from particular regions. Some of these have failed such as Thetford Forest in East Anglia (Gurnell et al., 2016b) while some have been successful such as on the Isle of Anglesey. According to Simberloff (2011), the probability of rapid re-invasion of the removed non-indigenous species must be low following eradication to have a chance of long term success. Significant isolation is evident in the case of Anglesey so recolonisation of the cleared area is easier to prevent (Gurnell et al., 2004). Post eradication, early detection and elimination of the invader is essential (Russell et al., 2007), while it is also more cost effective to intervene before the invader's density can increase (Leung et al., 2002). However, it is hard to detect low numbers so public and voluntary support may be required. This is the case on Anglesey, in which following the eradication of grey squirrels in 2013, a small number of sightings of grey squirrels on the island have been reported by members of the public and subsequently trapped (Shuttleworth, 2016). By fitting our model of the red/grey/squirrelepox system to the data from Anglesey, we have been able to include realistic grey squirrel control in the model (Chapter 4). This has enabled us to predict how much control is required to maintain a grey squirrel free population on Anglesey and to test strategies that could be used to expand the stronghold to include the mainland adjacent to Anglesey. Our predictions can be turned into a quantitative effort (in terms of trap days per year) which can be directly related to the actual resources required on the ground. Such information is vital for justifying ongoing conservation programmes and for applying for resources for future work. The model can also be used to estimate the cost of grey squirrel removal in other regions. For instance, the Cornwall Red

Squirrel Project aims to eradicate grey squirrels from The Lizard and West Penwith peninsula areas before introducing red squirrels there (Shuttleworth et al., 2015a). Our model could be used to determine the cost and therefore long-term viability of such a project.

Our mathematical modelling techniques could be used to determine which areas of a landscape would make suitable and relatively low maintenance strongholds. Strongholds in close proximity to neighbouring uncontrolled grey squirrel populations or forests with high broadleaved components require a significantly larger financial investment than very isolated red squirrel populations (Gurnell et al., 2004). By digitally mapping the real landscape, grey squirrels could be introduced into a large red only landscape. Tracking the replacement and movement of grey squirrels over time would highlight the pinch points in which greys disperse through to expand their range and also highlight the areas of the landscape in which grey squirrels would find it harder to reach/colonise due to poor dispersal corridors. Natural boundaries such as mountain ranges or large open spaces of moorland can provide excellent buffer regions around strongholds. Such isolated areas are therefore easier to maintain as red squirrel strongholds than areas in which grey squirrels can disperse to easily.

The island strongholds (excluding Anglesey) are largely free from the risk of grey squirrel invasion. Still, conservationists must be vigilant against rare invasion. For example greys squirrels have been known to stowaway in cars and ferries (Signorile, 2013) and squirrels could be released intentionally. Contingency plans must be in place to remove any grey squirrels that manage to get there (Gurnell et al., 2015; Shuttleworth, 2016). The island population of red squirrels on Brownsea Island also face a different threat. Here, leprosy has been detected though the impacts on mortality and the population dynamics are still unquantified. It is thought that the disease has been present on the island for at least 30 years and resistance to the disease in some squirrels is likely, though disease may make the population more vulnerable (Simpson et al., 2015; Dorset Wildlife Trust, 2016). There is also the possibility that squirrelpox could be accidentally introduced to island strongholds. Macpherson et al. (2016a) examined the likely impacts of a squirrelpox outbreak in the red stronghold on the Isle of Arran. They suggested that due to the relatively low density of red squirrels, squirrelpox would only spread locally and the infection would fade out. Thus, there would be some impact on red density in regions close to the initial outbreak but the disease would not spread extensively. Our modelling work for the Isle of Anglesey also confirms this finding (Chapter 4). Here, we showed that the infection would not spread through red only populations and was only likely to affect red densities in regions adjacent to grey squirrel populations that could support the disease. This suggests that the red squirrel strongholds on

islands should be resilient provided grey squirrels are prevented from establishing (should they manage to get to the islands).

It is approximated that 75% of the remaining red squirrels in the UK are found in the highlands of Scotland (Harris et al., 1995). Along the highland line, grey squirrel control is used to prevent the range expansion of grey squirrels. A key question that red squirrel conservation groups ask is where should grey control be applied along this interface and how much control is required. Mathematical models are useful tools to attempt to answer these questions. However, it has been difficult to parameterise the model to represent grey control due to a lack of suitable data. The parameterisation of the model using the comprehensive data set for the Isle of Anglesey (Chapter 3) has allowed the model to be used to try to answer these key questions. A recent study by White et al. (2017) has used the formulation developed for Anglesey to determine the level of grey control required along the highland line. This information is being used to direct future strategies and resource allocation.

Replacement of red squirrels by grey squirrels is also occurring in northern Italy following various introductions and translocations since 1948 (Bertolino et al., 2016). Protecting the native red squirrels did not become a relevant priority until the 1990s (Bertolino and Genovesi, 2005), and it was not until the past 10 years that intensive projects have been undertaken following issues with animal rights organisations during a trial eradication in 1997 (Bertolino and Genovesi, 2003). With predictions that grey squirrels will spread into Switzerland, France and then beyond, European authorities have funded two LIFE projects to try to control the range expansion of grey squirrels in Italy (Bertolino et al., 2016). As in 1997, a significant proportion of the public in areas in which trapping has been taking place do not support the intervention. Residents of the area like the novel, sociable grey squirrel so are against killing them. Therefore, surgical sterilization is being used in some sites to reinforce positive messages about the project in response to issues raised (Bertolino et al., 2016). This method is difficult to implement and costly but has been successful in an urban park in Genoa Nervi (Italy) from which the squirrels were trapped and released in a different park elsewhere. It is thought that this method will only work on populations up to 250 - 300 squirrels so it is not a large scale solution (Bertolino et al., 2016). Another non-lethal method considered in Italy is immunocontraception, but this can only be used to reduce population densities, not for eradication, and field application would be difficult when red squirrels are also present (Bertolino et al., 2016). Neither of these methods are currently being used in the UK as public support for the protection of strongholds using grey squirrel control is high.

The red squirrel protection described above has largely relied on the control of grey squirrels through trapping and removal. However, there is evidence of natural grey squirrel control occurring due to predation by the native pine marten (*Martes*

martes). The recovery of previously declined pine marten populations (due to persecution and loss and fragmentation of woodland) into areas in which grey squirrels now inhabit could lead to a decline in grey squirrel numbers. Since the grey squirrel introduction into the UK, it is thought that their habitat has not overlapped significantly with that of pine martens. Red squirrels and pine martens co-evolved and can exist in the same habitable regions. In Ireland, mammal distribution surveys have shown grey squirrels to be declining in an area in which pine marten populations have increased to high levels (Sheehy and Lawton, 2014). In 2007, grey squirrels were absent from some areas of Ireland (Irish Midland counties of Laois, Offaly, Cavan) in which they had previously inhabited, while pine marten numbers were high in these counties (Carey et al., 2007). A follow up study in 2012 showed that since 2007, grey squirrels had retracted further in range (Lawton et al., 2015). Furthermore, red squirrels had recolonised some areas in which they had previously been locally extinct. This grey decline and red increase is thought to be a result of a strong negative association between the grey squirrel and the pine marten (Sheehy and Lawton, 2014). This may be due the existence of a ‘landscape of fear’ (Laundrè et al., 2001) where grey squirrels avoid regions that are occupied by pine marten. Grey squirrels could also be more susceptible to predation due to ‘prey naivety’ (Sheehy, 2013). While red squirrels were observed to avoid feeders in which pine martens visited in a study in Northern Ireland, pine marten scent did not deter grey squirrels (David Tosh, unpublished data). However, grey squirrel awareness to pine martens may develop overtime and therefore reduce the level of predation. Meanwhile, grey squirrels continue to expand their range in other areas in Ireland in which pine martens are present so potentially there is a threshold density of pine martens required to induce prey switching in the pine marten (Sheehy and Lawton, 2014). Further research is needed to establish what densities of pine martens could be achieved in the UK and whether the conditions may lead to the same effect as observed in the Irish Midlands. A pilot pine marten reinforcement scheme is currently under way in Wales and the University of Aberdeen is planning similar field studies for the Scottish borders (Macpherson et al., 2016b).

Finally we turn our attention to the role of squirrelpox in the protection of red squirrels in the UK. While the spread of the invader can be controlled, in disease-mediated invasions, the infection may spread ahead of the wave of replacement (see Bell et al. (2009) and Chapter 5) and so disease could have an impact on the native population in the absence of the invader. Bell et al. (2009) showed that during the invader expansion, the disease can spread through the native population, decimating population numbers and thus reducing competitive pressure for the invader to colonise and replace the native. This has been observed to be happening in the red/grey squirrel system in certain areas but not universally (White et al., 2016a;

Chantrey et al., 2014). Squirrelepox is likely to be of most significance in high density, good habitat regions and so it is likely that disease-mediated invasion played a key role in the rapid spread of grey squirrels through southern and central England. In Scotland, Wales and Ireland, the potential density of grey and red squirrels is lower and squirrelepox may not be supported in grey squirrels or may show variations in prevalence (Goldstein et al., 2014; Jones et al., 2016). In this thesis, we showed that infection may not have persisted in grey squirrel populations as they expanded onto Anglesey between 1962 and 1998 (Chapter 3). It was only after their range expanded and abundance increased that the disease became more established. Support of this finding was observed in field data of expanding ranges of grey squirrels in Ireland within which low sero-prevalence has been found (Stritch et al., 2015). Our findings (Chapter 5) also showed that the disease may be too virulent to travel ahead of the wave of replacement into the red only population due to stochastic fade-out. This questions whether squirrelepox is still a key factor in red squirrel replacement. We have shown that squirrelepox is still likely to play a significant role in speeding up red replacement by causing epidemic outbreaks in red squirrels at the wave front. The competitive ability of the red squirrels at the interface is therefore reduced and invasion is mediated. Therefore, our work suggests that squirrelepox will not spread through the remaining red only populations in the UK but could play a significant factor at the interface between established red and grey squirrels. This therefore calls for squirrelepox to be prevented from spreading northwards in Scotland where it could reach the grey squirrel population along the highland red squirrel protection line. It also has implications for conservation of red squirrel stronghold populations. Our work modelling the control of grey squirrels to protect red populations on Anglesey showed that grey squirrel incursions can still occur (Shuttleworth, 2016). Squirrelepox transmission to red squirrels can therefore also occur. However, it is predicted to have minor effects on the total Anglesey population, confirming previous model findings in which outbreaks in red squirrel populations in protected stronghold regions are short-lived, with red squirrel abundance returning to pre-infection levels following disease fade-out (Chantrey et al., 2014; Macpherson et al., 2016a; White and Lurz, 2014; White et al., 2014, 2016a,b). This is particularly true in low density, fragmented habitat like Anglesey (and many of the parts of the UK that still have red squirrels). Focus should therefore be on grey squirrel control in and around stronghold populations rather than on preventing the spread of squirrelepox.

We should note that our work on the importance of squirrelepox assumes direct transmission of the disease between susceptible and infected individuals. The reality is that the transmission routes of the disease are still unknown. Spreading through scratches in the skin or mouth, through bites from ectoparasites (such as fleas and

ticks) or through scent markings and feeding areas are possible transmission routes (McInnes et al., 2016). The latter two require environmental contamination which presumes that the virus can survive for prolonged periods of time in the environment (McInnes et al., 2016). The importance of ectoparasites in squirrelpox transmission has been investigated in Cowan et al. (2016). SQPV scenarios with and without ectoparasite vectored transmission were modelled in a closed theoretical environment. Cowan et al. (2016) concluded that the presence of ectoparasites was essential for the persistence of SQPV in grey only squirrel populations and for justifying the sustainability of high levels of prevalence observed in some field studies. As this was modelled in a relatively small, closed environment, further work is required to confirm this hypothesis as other ecological mechanisms (such as spatial structure) can also promote the long-term persistence of squirrelpox.

In some red squirrel stronghold populations that are protected from grey invasion, squirrelpox epidemics have still occurred. There is evidence that red squirrels have survived infection (Chantrey et al., 2014). This suggests that red squirrels could evolve resistance to squirrelpox. A study by García-Ramos et al. (2015) showed that if the native species could evolve resistance to a virulent disease then, under certain circumstances, the native species could reverse the invasion of the non-native species. This requires that the native species is a better competitor than the invader in the absence of the infection, which may only be relevant for red squirrels in large coniferous forest habitats. This offers hope that in the long-term the impact of squirrelpox may diminish. Exploring the evolution of native species in response to infections introduced by invasive species is a topic for future research.

6.2 Conclusion

In this thesis we have shown that mathematical modelling can be used to understand the population and epidemiological dynamics of native invader systems that share an infectious disease. Our work has implications for understanding the spread of invasive species in general. We have also adapted the models to consider the case study system of the invasion of grey squirrels and replacement of red squirrels in the UK. Our work is useful for informing policy and conservation strategies to protect the remaining red squirrels in the UK. In general, this thesis shows that mathematical models are powerful tools for the conservation management of native species under threat from invasion.

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